

**The effect of terrestrial rodents on seed fate of hornbill-
dispersed plants in Pakke Tiger Reserve**

A Thesis Submitted to

The Manipal University

In partial fulfillment for the degree of

Master of Science
in Wildlife Biology and Conservation
2008

By

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Declaration

I declare that the thesis entitled "The effect of terrestrial rodents on seed fate of hornbill-dispersed plants in Pakke Tiger Reserve" comprises research work done by me under the guidance of Dr. Aparajita Datta, and co-guidance of Dr. Kavita Isvaran. The work is original and has not been done earlier by anyone else. Part of this work, which is related to or similar to work done by other researchers, has been cited in this thesis at appropriate places. The results presented in this thesis have not been submitted previously to this or any other university for an M.Sc. or any other degree.

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Certificate

I declare that the thesis entitled "The effect of terrestrial rodents on seed fate of hornbill-dispersed plants in Pakke Tiger Reserve" comprises research work carried out by Velho Nandini Dias at the Centre for Wildlife Studies under my guidance, and the co-guidance of Dr. Kavita Isvaran, during the period 2007-2008, for the Degree of Master of Science in Wildlife Biology & Conservation of the Manipal University. The results presented in this thesis have not been submitted previously to this or any other university for an M.Sc. or any other degree.

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EXECUTIVE SUMMARY

Research on the interactions between plants and their vertebrate dispersers is important to understand the consequences of seed dispersal in determining plant recruitment patterns. In the Paleotropics, the role of hornbills as primary seed dispersers has been well studied; however, there is poor understanding of the role that terrestrial rodents play in modifying the seed fate of several hornbill-dispersed plant species. While rodents are known to have positive effects on plant establishment through their scatter-hoarding behavior in the Neotropics, the impact of rodents as scatter-hoarders and secondary dispersers is poorly understood in the Paleotropics. Dispersers, through their seed deposition patterns, can exert evolutionary pressures on the life history traits of plants. Theoretical studies have explored the influence of seed deposition patterns on survival and recruitment strategies of seeds and seedlings, particularly their response under varying densities. Dispersers such as hornbills deposit seeds in either scattered or clumped conditions. These seed deposition patterns, which are later modified by rodents, determine conditions under which different plant species may have adapted to recruit and are likely to reflect in adult tree distributions. Thus tree species whose seeds are primarily dispersed in clumps are predicted to have lower density dependent mortality than those that are primarily scatter-dispersed. These species are predicted to have higher recruitment under the parent crown and greater levels of aggregation as adults.

This study, conducted at Pakke Tiger Reserve, Arunachal Pradesh from December 2007 to May 2008 had the following aims:

1) to investigate the influence of terrestrial rodents on seed fate of several hornbill-dispersed plant species, and understand their potential importance as secondary seed dispersers.

2) to examine whether density-dependent seed mortality due to predation varies across six hornbill-dispersed species, as a possible explanation for the variation in recruitment under parent trees and the resulting spatial dispersion and abundance of adult trees.

I quantified the impact of rodents on seed mortality and germination of five species by comparing exclosures that denied access to rodents, and plots where rodents were allowed access. Seeds were also marked under parent fruiting crowns and hornbill nest sites, and their fate monitored over time. I also set up camera traps to identify terrestrial rodents that modify seed fate.

The results of this study showed that rodents were mainly seed predators and not secondary seed dispersers. There were differential predation levels across species which had consequences for establishment. Further some species showed no difference in survival in the presence or absence of rodents. Nest sites of hornbills where seeds are deposited in clumps had greater per capita seed mortality compared to fruiting trees because of predation and possibly additional density dependent-mortality related to rotting. I also found that species differed in their ability to withstand density-dependent mortality, and that this has potential consequences for establishment and adult tree densities and distributions.

ACKNOWLEDGEMENTS

Ever stop to think, and forget to start again...

I'd like to thank the Arunachal Pradesh Forest Department for granting me permission to work in Pakke. I also wish to thank the DFO of Pakke Tiger Reserve, Mr. Nani Sha, for the logistic support. His team (range officers, beat officers, forest guards and watchers) have assisted me in innumerable ways during my stay.

I'd like to acknowledge the financial help provided by the Wildlife Conservation Society - India program and the Centre for Wildlife Studies for administrative support. The Manipal University for certifying the course and National Centre for Biological Sciences for academic support. I would also like to thank the Nature Conservation Foundation and the Centre for Electronics Design and Technology, Indian Institute of Science for the financial and logistic help. I'd like to thank Mr. Pittet and Shivaswamy for buying my bad phone network excuses and repeating many times how to use things as basic as a multimeter!

My field assistants have not only helped me in field but been partners in struggles and memories. I'd like to thank Rasham, Narayan, Tagge and Sher Bahadur for their assistance. I will always remember Kumar Thapa with fondness for his enthusiasm in field, good company and for his touching gestures like making rotis using a beer bottle as a rolling pin, for the divine when we were stuck with only potatoes and for making sure a glass of milk was always kept aside for his young son and me. I'd like to thank Lal Babu

and his family for not only always keeping their house open to us but telling us how to open it in their absence.

At my field station in Seijusa I am grateful to Kishore Dorje (and his family), who meant every single letter of ‘elder sister’, by being enthusiastic about my cooking disasters and for spending every evening with me teaching me how to burp and talk simultaneously, do break dance like exercises and other crazy things.

Ajith sir has been a mentor, friend and inspiration. He always allowed us freedom yet in ways that were inscrutable to us, he always ensured that we would be protected. He’s seen me through really bad first drafts and through thick and thin. I’d like to thank Rana for always being there, whether it was choosing books for me to read in field or convincing my father about letting me go to the north east. Jayashree Ratnam, Ravi Chellam, Kartik Shanker, Scot Duncan and Doug Levey took time off from their busy schedules to provide crucial inputs and help initially. Dr. M.S. Pradhan and Sanjay Molur helped with identification of rodents. I would like to thank Soumya Prasad for going out of her way to help me orient to a field that I was completely new to. Suhel Quader helped me frame the contours and contents of this dissertation, peer review my concept note and helped immensely in data analyses. I’d like to thank Geoff Hyde for helping me write and straight jacket my many stray thoughts. I’d also like to thank Rashid Raza for being like a ‘Dharamsala’ - not as quiet but for providing solitude, good food and peace of mind. I’d like to thank Goutam and Nandita for being accommodating and always keeping their house open. Despite my false promises of cooking pork, Robin Vijayan has not only

stayed up till 1:00 am in the morning to help provide inputs but seen me through my tears and weak moments. I'd like to thank Dev always being there to put a pen to paper for any conceptual doubt.

I'd like to thank my friends and classmates for their visits and support. Field work wouldn't have been half as exciting if I didn't get weekly letters from Kullu, Dharma, Swapna, Dipti, Umesh or Nachiket. Laughs, food and drinks were never short when Varun, Robin, Umesh, Milind and Karthik came to field. Rohit and Shashank for good company and lots of meat! Valmiki, Premila, Thelma, Mama, Sunith and Fernando ensured in unforgettable ways that Christmas, my birthday and stay in field was never lonely. To Umesh, who always thinks of me as a good egg even though he knows that I am slightly cracked!

I'd like to thank my guide and co-guide for always agreeing on data analysis, but more importantly for exposing me to a whole new world in ecology and teaching me how to think. I'd like to thank Kavita for always listening yet being insightful, being the calmest and composed among the three of us and for holding my dissertation together. It's difficult to express my gratitude to Aparajita. She's not only done more than most guides would for their students, but she's been like Santa Claus to an orphan child, a custodian through sticky times, a teenager through exciting findings and a friend through happy times. This dissertation would not have been doable without my father who worries too much yet always gives me wings to fly!



Establishment inside exclosure
Dysoxylum binectariferum



Wreathed Hornbill (*Aceros undulates*)
A primary seed disperser



Horsfieldia kingii, a large seeded hornbill
dispersed plant species



Seeds pigmented after hornbill dispersal
Pygeum acuminatum



A common seed predator, brush-tailed
porcupine (*Atherurus macrourus*)



A common seed predator, Himalayan
crestless porcupine (*Hystrix brachyura*)

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INTRODUCTION

Successful plant recruitment and establishment is often dependent on seed dispersal away from the parent tree (Howe and Smallwood 1982). Such dispersal, often animal-mediated in tropical forests, usually occurs as a two-step process. Primary dispersal by a large vertebrate species such as hornbills is often followed by secondary dispersal by smaller vertebrates such as terrestrial rodents, away from their primary deposition sites, thus re-arranging the seed shadows initially generated by primary dispersers (Stiles 1989).

Rodents could affect establishments through diverse behaviours such as predation, seed caching and seed dispersal. In many Neotropical forests, rodents are known to aid establishment by the non-recovery of caches and by reducing seed densities in highly aggregated clumps where survival would be compromised by various density-dependent mortality factors (Forget 1996, Pizo 1997, Forget et al. 2002, Jansen and Forget 2001).

In the Paleotropics, very little is known about how rodents modify seed fate, though Yasuda et al. (2000) and Cheng et al. (2005) have recorded scatter hoarding by rodents in Malaysia. Studies in South-East Asia have shown that genera such as *Hystrix*, *Leopoldamys* and *Bandicota* prey upon, scatter-hoard or defecate intact seeds (Yasuda et al. 2000, Kitamura et al. 2004, Yasuda et al. 2005).

Along with immediate ecological effects on the fate of seeds, dispersers, through their seed deposition patterns, can also exert evolutionary pressures on the life history traits of plants. In plant communities, species sometimes vary in their pattern of spatial distribution, some being

highly clumped, others scattered. One way in which this could come about is if seed deposition patterns for a particular species is clumped or scattered. For instance, clumped habitual latrines of the rhinoceros (*Rhinoceros unicornis*) and tapirs (*Tapirus terrestris*) are important recruitment sites for *Trewia nudiflora* and *Maximiliana maripa* (Dinerstein 1991, Fragoso 1997) respectively. Directed dispersal of the Neo-tropical plant species *Ocotea endresiana* by male bell birds (*Procnias tricarunculata*) is an example of seed dispersal that is scattered (Wenny and Levey 1998). Seeds of species that are deposited in aggregate ways by their animal dispersers may potentially have developed mechanisms to withstand density-dependent mortality factors and establish well even under clumped conditions. Scatter-dispersed seeds, will necessarily not have developed resistance to various density-dependent mortality factors as they normally recruit as isolated individuals (Howe 1989).

There are cases where seeds could be deposited in both scattered and clumped patterns.

Primary dispersers such as hornbills deposit seeds of the same plant species in both scatter (perch sites) and clumped conditions (nest trees and roost sites) (Datta 2001, Kitamura et al. 2004). Prior research in Pakke Tiger Reserve shows that though several species share hornbills as primary dispersers and these species vary greatly in the nature of adult tree spatial distribution (Datta 2001). These variations in adult tree distribution cannot be traced back to synchrony between the fruiting season of species and the period when hornbills deposit seeds in a specific manner.

For such a community, explanations need to be focussed on what occurs *after* seed deposition by primary dispersers. Post-dispersal processes influencing seed fate play an

important role in determining the spatial distribution of plant species (Janzen 1971, Hubbell 1980). For example, clumping of seeds is associated with attendant risks including increased seed predation (since vertebrate predators may use highly seed dense areas as feeding cues) (Janzen 1971). It is likely that clumped seeds of species evolve strategies to make them less attractive to seed predators, such as hard endocarps, production of secondary metabolites, or a faster rate of germination (Stiles 1989, Levey et al. 2002). Seeds that possess adaptations to counter such density-dependent factors are likely to establish and recruit under such conditions, which would lead to clumped adult tree dispersion. (Howe 1989).

In this study, I investigated:

1. The role of terrestrial rodents as secondary seed dispersers of five hornbill dispersed species. I examined differences in seed fates of these plant species at primary seed dispersal sites under hornbill nest trees and under parent fruiting trees.

:

2. Whether differential removal (and destruction) of seeds of six hornbill-dispersed species could be a possible explanation for the variation in spatial dispersion of adult trees of the six species.

The study was carried out between December 2007 to mid-May 2008 in Pakke Tiger Reserve (PTR), Arunachal Pradesh, north-east India. This reserve encompasses an area of 862 km². The vegetation of PTR is mainly classified as Assam valley tropical semi-evergreen forest (Champion & Seth 1964).

In order to examine the role of rodents in modifying seed fates of hornbill-dispersed plant species, I established rodent-proof metal exclosures under fruiting trees and nest sites. The fate of the seeds was monitored every three days till the establishment stage.

The variable effects of seed predation on establishment, recruitment and adult tree dispersion of six vertebrate-dispersed tree species was investigated using fifteen 1 m x 1m plots of in which seeds were set at varying densities. In addition, wedge- shaped plots from the base of the parent tree extending up to 30 m in length were sampled to enumerate the number seedlings and saplings under parent fruiting trees. Finally twenty two 50 m x 50 m vegetation plots were done to obtain a measure of adult tree dispersion.

I present the results of this study as two manuscripts. The first manuscript (Chapter 1) is titled ‘The effect of terrestrial rodents on seed fates of five hornbill-dispersed tree species in a lowland tropical forest in north-east India.’ In this manuscript, I attempt to understand the role of terrestrial rodents as secondary seed dispersers by tracking the fate of marked seeds of five hornbill-dispersed plant species. I examined the differences in seed removal and seed predation rates of five tree species whose primary dispersers are hornbills. I also examined differences in seed fates of these plant species at nest trees and under parent fruiting trees of each of these plant species. This manuscript is for submission to the *Journal of Tropical Ecology*.

The second manuscript (Chapter 2) is titled ‘Rodent seed predation: variable effects on establishment, recruitment and adult tree dispersion of six vertebrate-dispersed tree species ’.

In this manuscript, I examine whether predators have differential impacts on the seeds of the six hornbill-dispersed species, as a possible explanation for the variation in spatial dispersion of adult trees. In particular I focus on the differential removal of seeds by predators, along a wide spectrum of seed densities. This manuscript is also for submission to the *Journal of Tropical Ecology*.

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The effect of terrestrial rodents on seed fates of five hornbill-dispersed tree species in a lowland tropical forest in north-east India

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ABSTRACT

In Asian tropical forests, hornbills are important primary seed dispersers; however post-dispersal seed predation and/or caching by rodents may play an important role in modifying seed fate and determining plant establishment. Rodents may affect seed fates of plant species differentially since seeds of plant species vary in their vulnerability to rodent predation. In a tropical forest site in Arunachal Pradesh, India, I attempted to understand a) the role of terrestrial rodents as secondary seed dispersers by marking and tracking seeds fate of five plant species, b) their effect on seed fate by monitoring survival in the presence and absence of rodents using exclosures which prevented access to rodents. The experiments were conducted at two types of sites - under parent fruiting trees, and nest trees of hornbills. The results of this study showed that seeds of plant species had varying levels of seed predation and that high levels of seed predation had negative consequences for establishment. However, some species such as *Polyalthia simiarum* and *Chisocheton paniculatus* showed no difference in survival in the presence or absence of rodents. Seeds at hornbill nest sites showed lower survival compared to seeds under fruiting trees. Scatter-hoarding was rare and caused little re-arrangement in seed shadows at both sites, but differential seed predation had significant consequences for plant establishment.

KEYWORDS: hornbills, India, Paleotropics, scatter-hoarding, seed dispersal, seed predation

INTRODUCTION

Seed dispersers can exert evolutionary pressures on the life history traits of plants, as they determine the location where seeds are deposited and whether they subsequently establish and recruit in the population (Wenny 2001). Animal-mediated seed dispersal usually occurs through a two-step process. The first involves dispersal by ‘primary dispersers’, usually large-bodied vertebrate species such as hornbills. The second step is dispersal by ‘secondary dispersers’ following primary dispersal. Secondary dispersers are usually small-bodied species such as rodents. Both primary and secondary dispersers can exert selection pressures on plant species, and the nature of the interactions between, and impacts of primary and secondary dispersers have been well studied in the Neotropics, where secondary dispersers play an important role in characterizing the spatial dispersion of adult plants (Forget 1996, Forget *et al.* 2002). Rodents in particular can have diverse impacts on seed fates. They can limit establishment through seed predation (Wenny 2000), or enhance germination through multiple mechanisms, which include the non-recovery of caches and the decrease of density-dependent seed mortality by thinning, also mediated via predation (Forget *et al.* 1999, 2002, Pizo 1997, Wenny 1999).

The differential impact of rodent behaviour on seed fate is determined to a large extent by characteristics of the seed, such as hardness of the endocarp, concentration of secondary metabolites, and seed size (Stiles 1989). For instance, in the Neotropics, medium-sized seeds with a hard endocarp and a period of dormancy are more likely to be cached, whereas edible seeds which germinate faster are more likely to be preyed upon (Levey *et al.* 2002).

In the Paleotropics, secondary seed dispersal by rodents has been little studied. This would depend on the extent to which forest rodents in the Paleotropics scatter-hoard seeds and the subsequent fate of these cached seeds. A few recent studies have recorded scatter-hoarding by rodents such as *Leopoldamys* spp. in South-East Asia (Cheng *et al.* 2005, Yasuda *et al.* 2000, 2005). Other species such as *Hystrix brachyura*, *Niviventer* spp. and *Rattus* spp. are known to directly prey on seeds (Cheng *et al.* 2005, Kitamura *et al.* 2004 a).

In tropical Asia, hornbills are important primary dispersers of many forest tree species (Datta 2001, Kinnaird 1998, Kitamura *et al.* 2002, Kitamura *et al.* 2004 a, b). There is preliminary evidence to indicate that terrestrial rodents, through behaviours such as seed predation or caching, influence the fate of post-primarily dispersed seeds (Datta 2001, Cheng *et al.* 2005, Kitamura *et al.* 2004 a, Yasuda *et al.* 2000, 2005). The impact of predation or secondary dispersal by rodents on primarily hornbill-dispersed tree species remains poorly studied (Datta 2001, Kitamura *et al.* 2004 c). Through most of the year, hornbills disperse seeds in a scattered manner. During the breeding season, however, hornbills deposit seeds in clumps under nest trees. Seeds at nest sites (due to high seed densities) are expected not only to be subject to pressures such as pathogens and competition, but are also likely to attract seed predators such as terrestrial rodents.

In this study, I investigated the role of rodents as seed predators and secondary seed dispersers of five hornbill-dispersed tree species at nest sites (under which post-dispersal effects operated) and under parent fruiting trees (where seeds are undispersed) in a tropical forest in western Arunachal Pradesh, India. Preliminary observations also suggested that

there maybe differences in rodent food choice across different plant species in the area. Large-seeded species such as *Dysoxylum binectariferum* and *Horsfieldia kingii* were noted to have high predation levels, and no predation was observed on *Polyalthia simiarum* (Datta 2001). I therefore also examined the differences in seed predation by rodents across five hornbill-dispersed species and discuss the consequences of my findings for establishment and recruitment.

METHODS

Study site and species

This study was carried out between December 2007 and May 2008 in the tropical foothill forests of western Arunachal Pradesh in Pakke Wildlife Sanctuary and Tiger Reserve (92° 36' to 93° 09' E; 26° 54' to 27° 16' N). This reserve covers an area of 862 km² and is contiguous with the Eagle Nest Wildlife Sanctuary and Doimara Reserve Forest to the east, Papum Reserve Forest to the west and Nameri National Park to the south. The terrain is undulating and hilly with an altitudinal range of 150 to 1500 m above sea level (Datta 2001). Pakke Tiger Reserve has a tropical and sub-tropical climate, with a moderate winter from December to February, a pre-monsoon season from March to May and a monsoon season from June to September. The average annual rainfall is 2500 mm. The main vegetation type is classified as Assam valley tropical semi-evergreen forest (Champion & Seth 1964). A total of 343 woody species of angiosperms have been recorded, but at least 1500 vascular plants are likely to occur (Datta 2001, Datta & Rawat 2003). The area where the intensive study was carried out, had an approximate area of 9 km², and was located in the south-eastern part of the sanctuary. The most common hornbill-dispersed plant species are *Chisocheton paniculatus*, *Dysoxylum*

binectariferum, *Polyalthia simiarum* and *Amoora wallichii*. The altitudinal range of the intensive study site was 150 - 220 m above sea level.

Important avian frugivores in the study area are three species of hornbills - Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Aceros undulatus*) and Oriental Pied Hornbill (*Anthracoceros albirostris*). Other important avian frugivores include eight species of bulbuls (*Pycnonotus* spp.), five species of mynas (*Acridotheres* spp.), two species of imperial pigeons (*Ducula* spp.), four barbet species (*Megalaima* spp.), two leaf bird (*Chloropsis* spp.) species, Asian Fairy Bluebird (*Irena puella*), and two oriole species (*Oriolus* spp.) (Birand & Pawar 2004, Datta *et al.* 1998). At least 13 species of green pigeons, parakeets and doves occur in the area. However these species are known to be mainly seed predators (Jordano 1983, Lambert 1989, Walker 2007).

The pre-dispersal seed predators that occur include four species of diurnal tree squirrels (Himalayan striped squirrel *Tamiops macclellandi*, Hoary-bellied squirrel *Callosciurus pygerythrus*, Pallas red-bellied squirrel *Callosciurus erythraeus*, and the Malayan giant squirrel *Ratufa bicolor*). Although no surveys have been carried out to determine the terrestrial rodent community, there are 24 species of terrestrial rodents known from the evergreen and semi-evergreen forests of this region. Among the species that are known to occur in the area, the Himalayan crestless porcupine (*Hystrix brachyura*), Himalayan rat (*Rattus nitidus*), Norway rat (*Rattus norvegicus*), *Bandicota* spp. and *Niviventer* spp. are reported to prey on seeds, while *Leopoldamys* spp. has been reported to be a seed predator that also scatter-hoards (Cheng *et al.* 2005, Yasuda *et al.* 2000, 2005).

The five plant species listed below (Table 1) are among the most important non-fig species in the diet of hornbills in the area (Datta 2001, Datta & Rawat 2003). Preliminary observations indicate that several of these hornbill-dispersed species are preyed upon by rodents (Datta 2001). During the winter (December - January), *Pygeum acuminatum* was the only species fruiting along with *Polyalthia simiarum*. Fruiting of *Dysoxylum binectariferum*, *Chisocheton paniculatus* and *Horsfieldia kingii* occurred from February to May. The main fruiting period of *Polyalthia simiarum* was from May to July, while some fruiting also occurred from December to February. It was the only species that fruited throughout the study period.

Table 1. Fruit and seed characteristics of five hornbill dispersed plant species selected for the study arranged in order of fruiting time (Datta 2001, Datta & Rawat 2003).

Plant species	Family	Fruiting period	Seed weight (g)	Seed diameter (mm)		Fruit type
				Length	Width	
<i>P. simiarum</i>	Annonaceae	Dec-Feb; May-July	1.82	20.2	12.3	Fleshy single-seeded drupe
<i>P. acuminatum</i>	Rosaceae	Nov-Feb	4.3	20.6	15.1	Fleshy single-seeded drupe
<i>H. kingii</i>	Myristicaceae	Feb-May	7.84	35.7	20.1	Lipid-rich arillate capsule
<i>D. binectariferum</i>	Meliaceae	Feb-May	6.65	32.3	24.6	Lipid-rich arillate capsule
<i>C. paniculatus</i>	Meliaceae	April-July	7.99	31.7	23.9	Lipid-rich arillate capsule

Exclosure experiments: At parent fruiting trees and hornbill nest trees (a type of primary seed deposition site)

In order to understand the role of rodents in modifying and determining seed fates of plant species, I established rodent-proof metal exclosures (1m x 1m, height 1.4 m) under six to

twelve parent fruiting trees of each of the five study plant species. All exclosures were set up in a similar habitat type within the intensive study area. Fruiting trees of *Horsfieldia kingii* were rare in the intensive study site; therefore two exclosures for this species were set up twelve kilometers to the north-west of the intensive study site. Exclosures under parent fruiting trees were set up at different times, as and when fruiting of each species commenced. Seeds were handled using latex gloves to avoid leaving a scent of any kind. Ten seeds were placed inside each metal exclosure, while ten seeds were placed in an adjacent plot of the same size left open to rodents. Seeds left open to rodents were marked with a fishing line 40 cm in length (Forget 1990, Forget & Milleron 1991, Wenny 1999), while seeds inside the exclosures were not marked.

I also examined the effects of rodents on seed establishment at nest sites of hornbills, which are important primary dispersal sites. Hornbills regurgitate and deposit seeds of several species under nest trees during the breeding season (March to July). As this study period only partly coincided with the breeding season, I used the seeds of four species (*P. simiarum*, *H. kingii*, *C. paniculatus* and *D. binectariferum*) that are dispersed by hornbills and that were fruiting during the period (March to May). Since the densities of seeds were higher at nest trees, the number of seeds set out differed from those set out under parent trees. Twenty seeds of each of the four species were placed inside and outside rodent-proof metal exclosures, under six nest trees (two of Great Hornbill and four of Wreathed Hornbill). These seeds were placed 2.5 m away from the nest tree in separate exclosures for each species. All nest trees were of *Tetrameles nudiflora*, an emergent wind-dispersed species (Datta & Rawat 2004). During the study period, the exclosures set out across species and the replicates for

each species were staggered in time so that the differences in seed removal were not confounded by temporal variation across species.

Tracking seed fate

To determine whether rodents in the study area play an important role as secondary seed dispersers or predators, I marked the seeds that were left open to rodents in the experimental plots under both parent fruiting trees and nest trees. Seeds were marked with a 40 cm long fishing line (Forget 1990, Forget & Milleron 1991, Wenny 1999). If the fishing line was removed from the seed and remnants of the seed remained, it was classified as eaten. If the seed was transported away from the experimental plot, it was classified as cached. The fate of these marked seeds (i.e. preyed upon on-site, cached or remaining) was monitored every three days. The seeds were monitored till establishment, which was defined as the emergence of cotyledons. Seed mortality due to other factors, such as pathogen attack or rotting, was also noted. At the end of the study, seeds that remained were examined, and classified as hollow, solid or infested by insects. Seed viability of solid seeds was ascertained using the Tetrazolium dye test (Malone 1967). Seeds that were transported away and cached were also monitored to determine various seed fates (retrieved and eaten, germinated, not retrieved and viable, not retrieved and dead).

Camera traps and seed removal

In order to establish the identity of rodent visitors, and to monitor how they handle seeds, I also marked additional seeds that were placed in front of remotely triggered passive-infrared digital camera traps. The camera traps were modified to take four pictures a minute with a

minimum delay of 15 seconds when an animal passed in front of the sensor. The time and date could be set and the camera operated continuously for 24 hours. Three camera traps were set up under three fruiting trees of each of the five tree species. At each site, initially, eight seeds were marked for the camera. The seeds of each species were monitored every day for twenty days and replenished as and when the fate of all these marked seeds was modified. If seeds were cached, their fate was tracked till the end of the study period.

Statistical analyses

All statistical analyses were carried out using the statistical software R (version 2.6.1) (R Development Core Team 2007). As the data did not meet assumptions required for parametric tests (normality, equal variances), I used a Wilcoxon matched-pairs signed-rank test to compare the proportion of seeds viable inside and outside exclosures at parent fruiting trees and at nest trees for each species.

To examine variation among tree species in seed removal by rodents I used a linear model with normal errors with the difference in proportion viable inside and outside the exclosures as the response variable, and tree species and tree type (nest/ fruit tree) as the explanatory variables. Post-hoc pair wise comparison tests (Tukey's Honest Significant Difference Test) were used to examine differences between species pairs.

RESULTS

Exclosure experiments: At parent fruiting trees and hornbill nest trees

At fruiting trees across all five species, a total of 1000 seeds were set up, with a total of 500 inside the exclosures and 500 outside. Inside exclosures across all species, 272 out of 500 seeds survived (percent viable = 54.4). *P. acuminatum* had the highest percentage of seeds viable inside the exclosure (70%) while *H. kingii* had the lowest percentage (25%). However, across all species in the plots outside exclosures only 127 out of the 500 seeds survived (percent viable = 25.4). Across species, *C. paniculatus* and *P. simiarum* showed the lowest predation (3% and 18.13% respectively). No significant difference was observed in the proportion of seeds viable inside and outside exclosures for *P. simiarum* and *C. paniculatus*. I observed a significant difference in the proportion of seeds viable inside and outside exclosures for *D. binectariferum*, *P. acuminatum* and *H. kingii* (Table 2).

Table 2. Proportion of seeds viable for five plant species inside exclosure (n = 10 seeds) and outside (n = 10 seeds) under parent fruiting trees (Wilcoxon matched pairs signed rank test, significant results in bold). N = number of replicates.

Plant species	Proportion of seeds viable				z value	p
	Inside		Outside			
	Median	Inter-quartile range	Median	Inter-quartile range		
<i>D. binectariferum</i> N = 12	0.6	0.6 - 0.8	0	0	-2.965	0.03
<i>C. paniculatus</i> N = 10	0.55	0.47 - 0.7	0.6	0.57 - 0.63	- 0.943	0.943
<i>H. kingii</i> N = 6	0.25	0.2 - 0.3	0	0	-2.251	0.024
<i>P. simiarum</i> N = 12	0.4	0.25 - 0.5	0.4	0.3 - 0.5	-0.09	0.928
<i>P. acuminatum</i> N = 10	0.65	0.6 - 0.82	0.1	0 - 0.32	-2.831	0.05

At nest trees, a total of 960 seeds were set up, with 480 seeds set up inside the exclosures and 480 outside. Of the 480 seeds set up inside exclosures, only 138 seeds were viable (percent viable = 28.7) and outside only 39 seeds were viable (percent viable = 8).

A significant difference was observed in the proportion of seeds viable inside and outside exclosures for *D. binectariferum* and *H. kingii* (Table 3). The other two species showed no difference.

Table 3. Proportion of seeds viable for four plant species inside exclosure (n = 20 seeds) and outside (n = 20 seeds) exclosures under six hornbill nest trees (Wilcoxon matched pairs signed rank test, significant results in bold). N = number of exclosures

Plant species	Proportion of seeds viable				z value	p
	Inside		Outside			
	Median	Inter-quartile range	Median	Inter-quartile range		
<i>D. binectariferum</i> N = 6	0.72	0.64 - 0.77	0.07	0 - 0.15	-2.201	0.028
<i>C. paniculatus</i> N = 6	0.27	0.19 - 0.4	0.2	0.17 - 0.27	-1.725	0.084
<i>H. kingii</i> N = 6	0.074	0.05 - 0.08	0	0 - 0.02	-2.226	0.026
<i>P. simiarum</i> N = 6	0.1	0 - 0.11	0.15	0 - 0.21	-1.134	0.257

Out of the total seeds (980 marked seeds) at fruit and nest trees, 54.5% of the seeds were predated on. At parent fruiting trees 57.8 % of the seeds were preyed upon, while 51.5% of all seeds were preyed upon at nest sites. However the number of seeds rotten at nest sites was higher than at fruiting trees (Fig. 1).

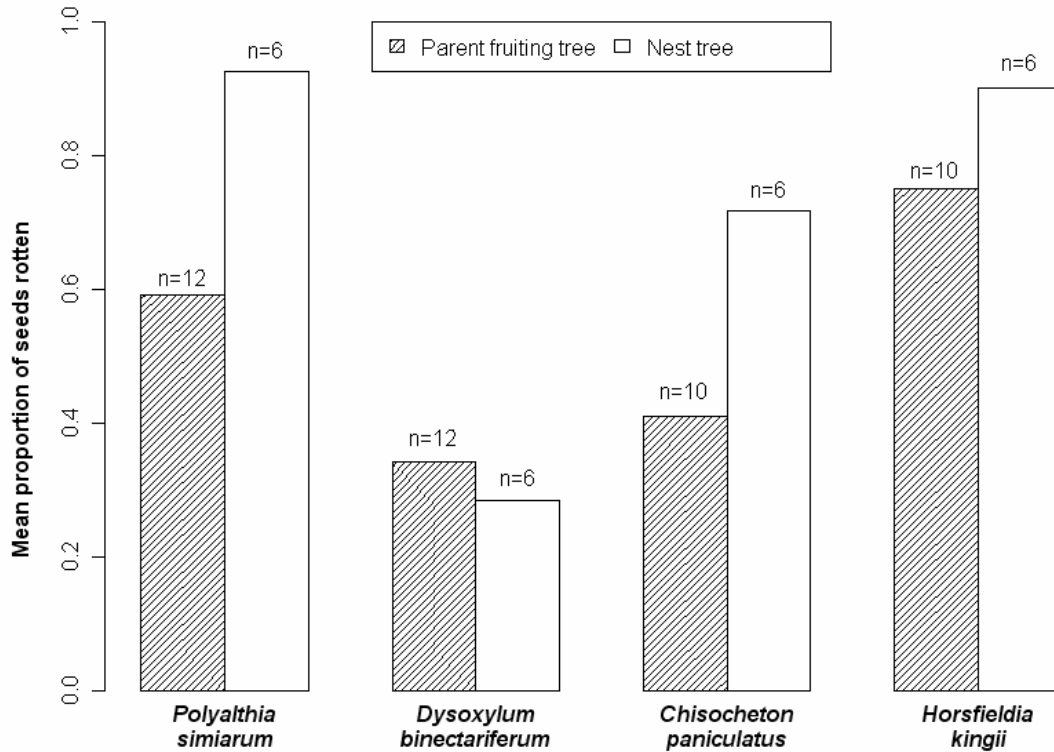


Figure 1. Mean proportion of rotten seeds inside exclosures at nest versus fruiting trees. 'n' indicates number of exclosures.

Across all tree species, only 20 seeds of three species were cached (*D. binectariferum*, *P. simiarum* and *P. acuminatum*) and of these, only three seeds of a single species (*P. acuminatum*) germinated. All other cached seeds were retrieved and eaten.

I also marked 410 seeds of all four species at fruiting trees (for camera traps). Therefore, a total of 1390 seeds (980 seeds marked for exclosure experiments from nest and fruit trees) were marked during the entire study. Most of these marked seeds were preyed upon (Fig. 2).

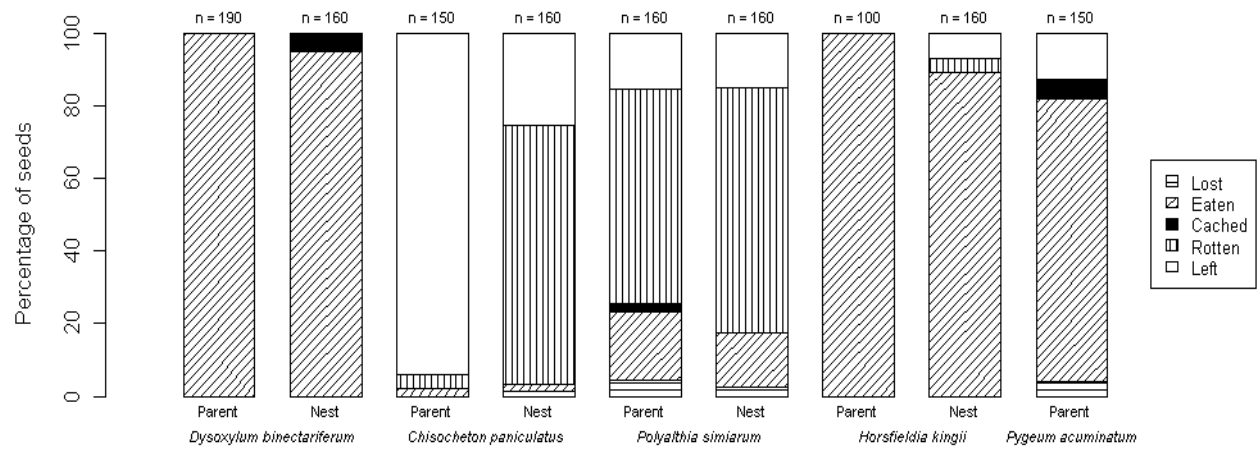


Figure 2. Fate of marked seeds of five plant species under parent trees and nest trees that are modified by terrestrial rodents. The total number of seeds is inclusive of those set up at camera traps.

Comparisons between hornbill nest trees and parent fruiting trees for species

Across nest trees and parent fruiting trees, proportion of seeds viable inside and outside exclosures showed differences for *H. kingii* and *D. binectariferum* (Fig. 3). Using a linear model with normal errors, overall across tree type and species, only tree species explained variation in the difference in proportion viable inside and outside exclosures ($F_{\text{Species}} = 53.18$; $p < 0.001$; $F_{\text{Tree type}} = 0.61$; $p = 0.43$). To determine which species pairs showed significant differences, we carried out post-hoc pair-wise comparisons. There were differences between *D. binectariferum* and *C. paniculatus*, *D. binectariferum* and *P. simiarum*, *H. kingii* and *P. simiarum* (Table 4).

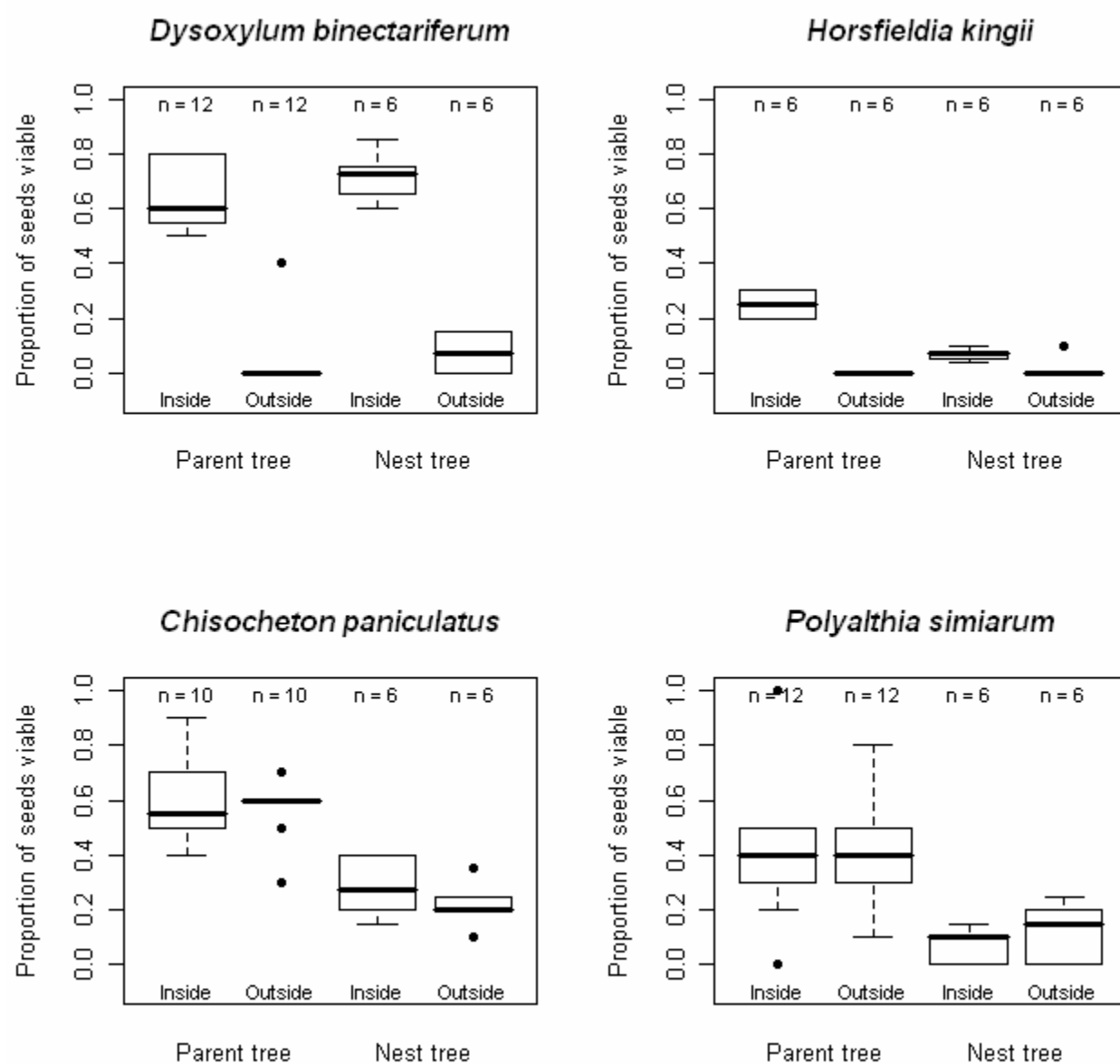


Figure 3. Proportion of seeds viable for species inside and outside exclosures at nest and fruiting trees. n = number of exclosures

Table 4. Pair-wise comparisons between species, of the difference in proportion viable inside and outside exclosures at fruit and nest trees (Tukey's Honest Significant Difference Test, significant results in bold). Difference = Species 1 (Proportion viable inside - outside) minus Species 2 (Proportion viable inside - outside)

Species pair	Difference	Lower CI	Upper CI	p
<i>Dysoxylum-Chisocheton</i>	0.60	0.44	0.75	0.00
<i>Horsfieldia-Chisocheton</i>	0.12	-0.05	0.29	0.26
<i>Polyalthia-Chisocheton</i>	-0.05	-0.20	0.11	0.85
<i>Horsfieldia-Dysoxylum</i>	-0.48	-0.65	-0.31	0.00
<i>Polyalthia-Dysoxylum</i>	-0.65	-0.80	-0.50	0.00
<i>Polyalthia-Horsfieldia</i>	-0.17	-0.34	0.00	0.05

Camera-traps and seed removal

Through camera-trapping, I determined the identity of rodent visitors. I found that for highly preyed upon species, such as *D. binectariferum*, *H. kingii* and *P. acuminatum*, the Himalayan crestless porcupine and the Brush-tailed porcupine consumed the maximum proportion of seeds (Table 5). These two species appeared to prey on seeds directly on-site. For species such as *P. simiarum* that were not highly preyed upon, only one species (*Niviventer* spp.) was seen to prey on a small proportion of these seeds. During the 20 day trapping period, no vertebrate was seen consuming seeds of *C. paniculatus*.

The other species of rodent that were recorded at camera traps preying on seeds were tentatively identified as *Rattus* spp. and *Berylmys* spp. and the Hoary-bellied squirrel (*Callosciurus pygerythrus*). The only other mammalian visitor recorded in these traps was the large Indian civet (*Viverra zibetha*).

Table 5. Summary of proportion of seeds preyed upon by rodents based on camera trap records from the 20 day sampling period

Plant species	% of seeds eaten	% eaten by single species	Main seed predator
<i>D. binectariferum</i>	100	77	Himalayan crestless porcupine
<i>P. simiarum</i>	25	25	<i>Niviventer</i> spp.
<i>H. kingii</i>	100	82	Brush-tailed porcupine
<i>P. acuminatum</i>	100	33	Brush-tailed porcupine
<i>C. paniculatus</i>	0	0	None observed

DISCUSSION

The results of my study show that terrestrial rodents modify seed fate of some hornbill-dispersed plant species mainly by preying on seeds. Scatter-hoarding behavior and caching, which could result in effective secondary dispersal, were very uncommon. Camera-trap monitoring also corroborated this, where most species were observed to be preyed on directly by a few rodent visitors.

Only 1.43% of marked seeds were cached and most of these were subsequently retrieved and eaten. Other studies in the Paleotropics also report little evidence for caching leading to effective secondary dispersal. Cheng *et al.* (2005) and Yasuda *et al.* (2000, 2005) recorded evidence for scatter-hoarding in South-east Asia. However, most of these cached seeds were subsequently preyed upon. Cheng *et al.* (2005), found that only the Edward's long-tailed rat (out of four species compared) scatter-hoarded seeds, of which only a small proportion germinated. These results suggest that terrestrial rodents may not be important secondary seed dispersers in this region as seed caching behavior is limited. This is contrary to Neotropical patterns of high levels of scatter-hoarding and positive relationships between

scatter-hoarding by rodents and plant establishment (Jansen & Forget 2001). The differences in caching (between the Neotropics and Paleotropics) maybe related to the availability of resources throughout the year. In the Neotropics, most scatter-hoarding is seen during the wet season when most plant species are fruiting. These cached seeds are depended on during periods of food scarcity (Forget *et al.* 2002). In Pakke Tiger Reserve, while there are seasonal differences in resource availability, there is a lean fruiting period (in terms of overall fruiting intensity) from August to January. Species such as *P. simiarum* and *P. acuminatum* and several tree species belonging mainly to the family Lauraceae (*Actinodaphne* spp., *Alseodaphne* spp., *Beilschmedia* spp., *Litsea* spp.) fruit during this period (Datta 2001). An alternative explanation is that rodents may show seasonal and annual variations in scatter-hoarding behaviour. Scatter-hoarding behaviour and levels may have been low as the study was mainly during the relatively resource-rich period (January to May). A longer duration study spanning the entire year may be needed to conclusively understand patterns of scatter-hoarding.

Predation rates on seeds vary among hornbill dispersed plant species. Species such as *C. paniculatus* and *P. simiarum* were preyed upon much less by rodents compared to species such as *D. binectariferum* and *H. kingii*. As a result, for these species (that had low predation levels), there was no significant difference in the proportion of seeds viable inside and outside exclosures. This may be explained by the intrinsic properties of the seeds of these species. *Polyalthia longifolia* (a closely-related congeneric species) is known to have cytotoxic organic compounds and seed extractions have yielded antibacterial activities (Faizi *et al.* 2003).). Even related species (*D. binectariferum* and *C. paniculatus*) from the same

family, Meliaceae, showed varying predation levels. *C. paniculatus* contains chemical compounds called limonoids that could dissuade vertebrates from consuming their seeds (Pannel & Koziol 1987). Further, a hard endocarp may decrease seed predation by vertebrates (Stiles 1989). Consistent with this, *C. paniculatus* has a hard endocarp unlike *D. binectariferum*. However, Datta (2001) had recorded relatively high seed predation levels on *C. paniculatus* (72%). It is likely that levels of rodent seed predation vary temporally. The fruiting period of this species is from April-July and our study extended only up to early May.

The differential rates of seed predation could have several consequences for the life history strategies and patterns in abundance and distribution of these plant species. Datta (2001) documented the abundance of some hornbill-dispersed plant species in the habitat. *P. simiarum* is one of the most abundant species ($21.8 \text{ trees ha}^{-1} \pm 4.71 \text{ S.E.}$) in the habitat; fruits are available for nine months a year and eaten by several vertebrate dispersers. Two species from the family Meliaceae also had differing densities of adult trees in the habitat. *C. paniculatus* had lower predation levels and was more abundant ($21.52 \text{ trees ha}^{-1} \pm 1.36 \text{ S.E.}$) compared to highly preyed upon species like *D. binectariferum* which occurred at much lower densities ($4.19 \text{ trees ha}^{-1} \pm 1.36 \text{ S.E.}$). Species such as *H. kingii* and *P. acuminatum* also showed very high levels of predation and low adult densities ($1.14 \text{ trees ha}^{-1} \pm 0.62 \text{ S.E.}$ and $1.71 \text{ trees ha}^{-1} \pm 0.71 \text{ S.E.}$). Dioecious species such as *H. kingii* are dependent on pollinators for fruit-set and are often pollinator-limited to a greater extent. For such a species it would be beneficial to have a conspecific at the nearest distance possible. However the high predation pressures limit establishment under parent fruiting trees, and therefore could have deleterious

impacts on reproductive fitness of this species resulting in rarity. The experimental study with marked seeds confirms that species such as *H. kingii*, *D. binectariferum* and *P. acuminatum* suffer high predation, while *P. simiarum* and *C. paniculatus* suffer low predation levels.

The advantages of escape from parent trees has been predicted by Janzen (1970, 1971) and Connell (1971). Under parent fruiting trees, seeds are likely to be prone to high mortality which is positively correlated with density and negatively correlated with distance (Wenny 2001). For all species except *P. simiarum* and *C. paniculatus*, we find partial evidence for the ‘escape hypothesis.’ Some of these seeds of these species are deposited under nest trees of hornbills. In this study I found that hornbill nest trees, thought to be important primary dispersal sites, were not particularly suitable for seed establishment. The high seed density at nest trees appears to lead to increased predation and rotting caused by density-dependent mortality. However, the comparison of seed fate between nest trees and parent fruiting trees was not a true comparison of the scenario under nest trees where the seed rain is an assemblage of many species, while parent fruiting trees necessarily had seed rain only from one species. Nevertheless, we found that the proportion of seeds found rotten inside exclosures for *P. simiarum*, *C. paniculatus* and *H. kingii* was many times higher than that found at fruiting trees. Although the per capita seed mortality is higher at nest trees, overall, the larger numbers of seeds may make the probability of at least one seed establishing higher and lead to overall higher numbers of seeds establishing. The escape hypothesis needs to be further explored along with the effect of deposition patterns on seed survival of species at varying densities under perch and nest trees of hornbills.

Rodents were predators and not secondary seed dispersers unlike in the Neotropics. There were differential predation levels across plant species with some plant species showing no difference in survival in the presence or absence of rodents. This variation in the effect of rodent predation has consequences for establishment. Primary dispersal sites such as hornbill nest sites may be associated with low seed survival compared to parent fruiting trees because of predation and increased density dependent mortality related to rotting. This study underlines the effects that rodent can have at the first stage on the structure and dynamics of forest tree communities.

ACKNOWLEDGEMENTS

This work was mainly funded by the Wildlife Conservation Society, USA. I thank the Nature Conservation Foundation, Mysore and the Centre for Electronics Design and Technology, Indian Institute of Science for logistic support and financial help. I also wish to thank the Arunachal Pradesh Forest Department for granting permission and facilitating the fieldwork. Kumar Thappa, Tagge Talang, Rajan Bahadur, Rasham Barra and Narayan Mogar made this work possible with their immense support in the field. I thank Suhel Quader and Ajith Kumar for help in data analyses.

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Rodent seed predation: variable effects on establishment, recruitment and adult tree dispersion of six vertebrate-dispersed tree species

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Running head: Effect of rodent seed predation on plant species

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ABSTRACT

In plant communities, species sometimes vary in their pattern of spatial distribution, some being highly clumped, others scattered. I examined the variable effects of rodent seed predation on establishment, recruitment and adult tree dispersion of six hornbill-dispersed tree species. I first examined whether rates of seed removal by predators show different density-dependent relationships across six species. I also examined whether differential removal by seed predators could explain the differences in the recruitment under the parent fruiting trees for each of the six species. Finally I used an index of adult tree dispersion, to examine the influences of differential predator removal and recruitment on adult tree distribution. Most species showed density-dependent mortality due to seed predation; however two species were not subject to density-dependent mortality. Species with the lowest seed predation levels such as *Chisocheton paniculatus* and *Polyalthia simiarum*, have the highest mean recruitment near parent fruiting trees and the most clumped adult tree dispersion. Seeds of species such as *Dysoxylum binectariferum*, *Canarium resiniferum*, *Pygeum acuminatum* and *Horsfieldia kingii* are highly preyed upon, show low recruitment and more spaced adult tree dispersion. This study also highlights the relative importance of dispersers such as hornbills in allowing seeds of highly preyed upon species to escape from density dependent mortality factors operating under parent trees.

KEYWORDS: density-dependence, hornbills, India, Paleotropics, seed predation, seed survival

INTRODUCTION

In plant communities, tree species vary in their pattern of spatial distribution, with some being highly clumped, while others are scattered. A plausible mechanism by which this could come about is if seed deposition patterns themselves vary along a continuum between clumped and scattered (Howe 1989). Following the predictions from Janzen (1970, 1971) and Connell (1971), many studies have assumed that seed survival in clumps is low, while scatter-dispersal has been considered to be better for seed establishment. This is based on the idea that density-dependent mortality would undermine survival and recruitment in clumps (Becker & Wong 1985, Clark & Clark 1984, Packer & Clay 2000). However, an increasing number of empirical studies have demonstrated that many species are deposited in aggregations by their primary dispersers and this is not always detrimental to survival. For instance, gorillas (*Gorilla gorilla*) deposit seeds in clumps at nests and seedling survival was shown to be higher when compared to other parts of the forest (Tutin *et al.* 1991). Clumped habitual latrines of the rhinoceros (*Rhinoceros unicornis*) and tapirs (*Tapirus terrestris*) are important recruitment sites for *Trewia nudiflora* and *Maximiliana maripa* (Dinerstein 1991, Fragoso 1997) respectively. For some Neotropical plant species such as *Ocotea endresiana* directed dispersal by male bell birds (*Procnias tricarunculata*) aids establishment (Wenny & Levey 1998). Seeds of species that are deposited in clumps should evolve defenses against density-dependent mortality factors, be able to recruit under high densities and adult tree species should be more common and have a highly clumped dispersion pattern. Seeds of species that are scatter-dispersed should not have developed resistance to density-dependent mortality factors and would recruit poorly under parent crowns, be rare and have a scattered adult tree dispersion pattern (Howe 1989).

Many tree species that are clump-dispersed are often the result of dispersal by primates or large herbivores (Dinerstein 1991, Tutin et al. 1991, Fragoso 1997, Russo & Augspurger 2004). However, there are cases where seeds of a given tree species could be deposited in both scattered and clumped patterns. This is true of tree species dispersed by large frugivorous birds such as hornbills that play an important role as primary seed dispersers in tropical forests (Kinnaird 1998, Whitney *et al.* 1998, Datta 2001, Poulsen *et al.* 2002, Kitamura *et al.* 2004). During most of the year hornbills are predominantly scatter dispersers. Seeds are regurgitated singly or in small groups at perch sites ($1 \text{ seed m}^{-2} \pm 0.16_{\text{SD}}$) (Datta 2001). However, at roost sites used by hornbills regularly, seeds are regurgitated and deposited in a clumped manner throughout the year. Roost trees are usually in open riverine habitats and are unlikely to be suitable microsites for recruitment of these species. During their breeding season (March to August) seeds of up to 35 species are also deposited in clumps under nest trees ($100 \text{ seeds m}^{-2} \pm 32.73_{\text{SD}}$), while seeds of these same species are also scatter-dispersed by foraging birds in the daytime (Datta 2001).

Thus, whether seeds are clump or scatter-dispersed is dependent on primary dispersers such as hornbills. Prior research in the study area shows that though several species share hornbills as primary dispersers, these species vary greatly in adult tree distribution and density. For example, *Polyalthia simiarum* occurs in clumps and has high densities ($21.8 \text{ trees ha}^{-1} \pm 4.71_{\text{SE}}$) whereas adults of species such as *Horsfieldia kingii* are scattered and rare ($1.14 \text{ trees ha}^{-1} \pm 0.62_{\text{SE}}$) (Datta 2001, Datta & Rawat 2003). The variable densities of adult trees cannot be explained by the type of deposition by hornbills alone. For instance, the fruiting peak

(February - May) of the most scattered species (*H. kingii*) directly overlaps with the period of greatest clumped deposition by hornbills i.e. the nesting period.

For such a community, explanations need to be focused on what occurs *after* seed deposition by primary dispersers. Seed fates may also be further modified by secondary dispersers/predators which move seeds from primary disperser deposition sites. These post-dispersal processes influencing seed fate may play an important role in determining the spatial distribution of plant species (Janzen 1971, Hubbell 1980). For example, clumping of seeds is associated with increased predation levels (since vertebrate predators may use highly seed dense areas as feeding cues) at the seed stage (Janzen 1971) or host specific pathogen attack (Packer & Clay 2000) and increased seedling and sapling competition (Wenny 2001). It is likely that clumped seeds evolve strategies to make them less attractive to seed predators, such as hard endocarps, production of secondary metabolites, or a faster rate of germination (Stiles 1989, Levey *et al.* 2002). Seeds that possess adaptations to counter such density-dependent factors are likely to establish, recruit under such conditions, which would lead to clumped adult tree dispersion (Howe 1989).

In this study, I examined whether density-dependent mortality due to predation varies across seeds of the six hornbill-dispersed species, as a possible explanation for the variation in spatial dispersion and abundance of adult trees. In particular, I have focused on the differential removal (and destruction) of seeds by predators, and examined if rates of seed removal show different density-dependent relationships across the six species, by exposing seeds of the six species to predator removal along a wide spectrum of seed densities.

Additionally, I have examined a different explanation for the variation in spatial distribution of the six species within my study area. While the recruitment of new trees for each species involves hornbills, this does not rule out other means of recruitment, which does not depend on a disperser or fit the Janzen-Connell predictions. In particular, all six species drop many of their fruits directly to the ground, underneath the canopy of the parent tree. If a sufficient number of these survive, this could result in a clumped dispersion of adult trees. Given sufficient variation in beneath-parent-tree mortality between the six species, this may partly explain the observed differences in adult tree distribution.

In this study, I have therefore examined:

- (1) whether there is differential removal by predators for different tree species at varying densities.
- (2) whether differential removal by predators could explain differences in the density of seedlings/saplings underneath the parent fruiting trees for each of the six species. I tested the prediction that species that show high density dependent mortality of seeds should show low recruitment under parent fruiting trees.
- (3) Finally I have attempted to link the patterns in seed survival and seedling recruitment to observed adult tree dispersions and densities of the six tree species (using an index of spacing).

Here I tested the predictions that (a) density dependent seed mortality should be negatively related to seedling recruitment under parent fruiting trees and (b) density dependent mortality should be negatively related and seedling recruitment under parent crown positively related to the degree of clumping of adult trees.

METHODS

Study site and species

The study was carried out between December 2007 and May 2008 in the tropical foothill forests of western Arunachal Pradesh in Pakke Wildlife Sanctuary and Tiger Reserve (92° 36' to 93° 09' E; 26° 54' to 27° 16' N). This reserve covers an area of 862 km² and is contiguous with the Eagle Nest Wildlife Sanctuary and Doimara Reserve Forest to the east, Papum Reserve Forest to the west and Nameri National Park to the south. The terrain is undulating and hilly with an altitudinal range of 150 to 1500 m above sea level (Datta 2001). The study area has a tropical and sub-tropical climate with a moderate winter from December to February, a pre-monsoon season from March to May and a monsoon season from June to September. The average annual rainfall is 2500 mm. The main vegetation type is classified as Assam valley tropical semi-evergreen forest (Champion & Seth 1964). A total of 343 woody species of angiosperms have been recorded but at least 1500 vascular plants are likely to occur (Datta 2001, Datta & Rawat 2003). The intensive study site was located in the south-eastern part of the sanctuary. The approximate area of the intensive study site was 9 km². The most common hornbill food plant species are *Chisocheton paniculatus*, *Dysoxylum binectariferum*, *Polyalthia simiarum* and *Amoora wallichii*. The altitudinal range of the intensive study site was 150 - 220 m above sea level. The forest in other areas is much wetter

and is dominated by *Mesua ferrea*, *Livistona jenkinsiana*, *Dillenia indica*, *Canarium resiniferum* and *Kydia calycina*.

The important avian frugivores in the study area are three species of hornbills - Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Aceros undulatus*) and Oriental Pied Hornbill (*Anthracoceros albirostris*). Other important avian frugivores include eight species of bulbuls (*Pycnonotus* spp.), five species of mynas (*Acridotheres* spp.), two species of imperial pigeons (*Ducula* spp.), four barbet species (*Megalaima* spp.), two leaf bird (*Chloropsis* spp.) species, Asian Fairy Bluebird (*Irena puella*), and two oriole species (*Oriolus* spp.) (Datta *et al.* 1998, Birand & Pawar 2004). At least 13 species of green pigeons, parakeets and doves occur in the area. However these species are mainly known to be seed predators (Jordano 1983, Lambert 1989, Walker 2007).

The pre-dispersal seed predators that occur include four species of diurnal tree squirrels (Himalayan striped squirrel *Tamiops maclellandi*, Hoary-bellied squirrel *Callosciurus pygerythrus*, Pallas red-bellied squirrel *Callosciurus erythraeus*, and the Malayan giant squirrel *Ratufa bicolor*). Although no surveys have been carried out to determine the terrestrial rodent community, there are 24 species of terrestrial rodents known from the evergreen and semi-evergreen forests of this region. Among the species that are known to occur in the area, the Himalayan crestless porcupine (*Hystrix brachyura*), Himalayan rat (*Rattus nitidus*), Norway rat (*Rattus norvegicus*), *Bandicota* spp. and *Niviventer* spp. are reported to prey on seeds, while *Leopoldamys* spp. has been reported to be a seed predator that also scatter-hoards (Cheng *et al.* 2005).

Study plant species

The six (non-fig) plant species listed below are among the most important species in the diet of hornbills in the area (Datta 2001, Datta & Rawat 2003) (Table 1). Preliminary observations indicated that several of these hornbill-dispersed species were preyed upon by rodents (Datta 2001). During the winter (December - January), *Pygeum acuminatum* and *Canarium resiniferum* were the only species that were fruiting. *C. resiniferum* does not contribute to a significant proportion of the hornbill diet (Datta & Rawat 2003). During the latter period from February to May, *Dysoxylum binectariferum*, *Chisocheton paniculatus* and *Horsfieldia kingii* started fruiting along with *Polyalthia simiarum* that continued to fruit throughout the study period.

Table 1. Fruit and seed characteristics of six hornbill dispersed plant species selected for the study arranged in order of fruiting time (Datta 2001, Datta & Rawat 2003).

Plant species	Family	Fruiting period	Seed weight (g)	Seed diameter (mm)		Fruit type
				Length	Width	
<i>C. resiniferum</i>	Burseraceae	Nov-Dec	3.55	34.7	15.9	Single seeded drupe
<i>P. simiarum</i>	Annonaceae	Dec-Feb; May-July	1.82	20.2	12.3	Fleshy single-seeded drupe
<i>P. acuminatum</i>	Rosaceae	Nov-Feb	4.3	20.6	15.1	Fleshy single-seeded drupe
<i>H. kingii</i>	Myristicaceae	Feb-May	7.84	35.7	20.2	Lipid-rich arillate capsule
<i>D. binectariferum</i>	Meliaceae	Feb-May	6.65	32.3	24.6	Lipid-rich arillate capsule
<i>C. paniculatus</i>	Meliaceae	April-July	7.99	31.7	23.9	Lipid-rich arillate capsule

Field methods

1. Measurement of seed removal rate within and across species at different densities.

Fifteen 1 x 1m plots of seeds of each of the six study tree species were set up at varying densities. I simulated seed densities that were chosen randomly from a range of one to hundred seeds per square metre. Each plot was set 50 m apart to ensure that the discovery of one plot by rodents did not increase the chances of finding other plots. All seeds were collected from under parent fruiting trees and set out in a similar habitat type within which I assumed homogenous predation and abiotic pressures. Latex gloves were used while collecting and placing seeds out for a given plot, to avoid leaving a scent of any kind. To decrease temporal variation in removal rate, seeds of available species were set out in batches together. The number of seeds removed were monitored every alternate day. Seeds that were removed were assumed to be preyed upon. This was a valid assumption as another experimental study with marked seeds carried out during the same period found that most seeds removed by rodents were preyed upon (see Chapter 1). Seed mortality due to other factors such as pathogen attack or rotting was also noted. The seeds were monitored till establishment, which was defined as the emergence of cotyledons. At the end of the study, the seeds that remained were examined and classified as hollow, solid or infested by insects. Seed viability of solid seeds was ascertained using the Tetrazolium dye test (Malone 1967).

2. Recruitment under parent fruiting trees

To quantify recruitment under parent fruiting crowns, I selected fruiting individuals of each of the tree species. For each tree species, at the base of each fruiting tree, I established a

wedge-shaped plot that was randomly directed at an angle of 20 degrees radiating 30 m from the tree base (Cordeiro & Howe 2003). Six to 10 replicates for each of the species was established. Seedlings were defined as plants that were below 40 cm in height, while all plants between 40 cm and 100 cm were considered as saplings. I counted all seedlings and saplings of each tree species within 2 m distance intervals starting from the base of the tree. I enumerated seedlings and saplings at the end of the fruiting period for each individual. The seedling/sapling population could have been a result of recruitment in previous years. It should be noted that seedling recruitment under parent fruiting trees is a result mainly of undispersed seeds from fruit/seed fall and is not due to deposition by hornbills, as nest tree species used by hornbills are wind-dispersed tree species such as *Tetrameles nudiflora*, *Ailanthus grandis* and *Altingia excelsa* (Datta 2001). However, some proportion of seeds under parent crowns could be dropped or regurgitated while feeding at parent fruiting trees. Hornbills are efficient dispersers (wide-ranging and known to disperse seeds over long distances) (Holbrook & Smith 2000, Holbrook *et al.* 2002, Whitney *et al.* 1998), therefore it is unlikely that a significant proportion of seeds are deposited directly below parent fruiting crowns.

3. Adult tree species density and dispersion

To determine adult tree species dispersion patterns of the selected tree species, twenty two 50 x 50 m plots were established at randomly selected locations, with twelve plots in the intensive study site and ten in adjoining areas. Of these ten plots, five were located twelve kilometers to the north-west and five were located eight kilometers north of the main study area. In each plot, the number of adult trees of the six species was enumerated. Adult trees

were defined as those with GBH ≥ 30 cm. I enumerated all individuals of each of the focal tree species in the plots to obtain densities of each tree species.

I obtained a measure of dispersion by using the Clark & Evans (1954) index for computing spatial dispersion. I calculated nearest neighbour distances of each individual tree to a conspecific tree in each plot. In cases where the nearest neighbour of a conspecific tree was outside the plot, the nearest distance was still measured. For some species like *H. kingii* and *P. acuminatum* where there were no conspecifics within or close to the plot, a GPS location of each tree located by searches in the intensive study site was marked to calculate nearest neighbour distance.

Analytical methods

Density dependent effects on seed mortality

I analysed the effect of seed density on the daily survival rate for the six tree species and the variation in this relationship across species. Data from the 1 x 1 m experimental plots were used to evaluate the effect of seed density on seed mortality. Daily survival rate was used as a measure of the per capita risk of mortality experienced by seeds. For each plot, daily survival rate was estimated from the count of the number of seeds surviving over time using a generalized linear model (GLM) with Poisson error structure and a log link (Crawley 2007). The number of seeds surviving was the dependent variable and the time in days was the independent variable. The slopes from these GLMs represent the log of daily survival rate for each plot.

I then modeled the effect of seed density and species on daily survival rate using a linear model (LM) with normal errors. Log daily survival rate (the slopes from the GLMs described previously) was used as the dependent variable while seed density and species were the independent variables.

Recruitment under parent fruiting trees

While recruitment was enumerated in 2 m intervals in each wedge-shaped plot under parent fruiting trees, I divided that data into near (0 - 10 m) and far (10 - 30 m) distance classes to examine the effect of distance from parent tree on recruitment. Due to low recruitment under parent fruiting trees, seedlings and saplings were pooled together for the analysis. A GLM with Poisson errors and a log link was used to model the effect of species and distance from parent tree on the number of recruits. Area was included as an offset in the GLM to take the unequal area (near and far) into consideration. As there was some over-dispersion and deviance of residuals from normality, non-parametric analyses were also run. A Kruskal Wallis One-Way ANOVA was used to compare the difference in the mean densities of recruits between near and far distance classes across species. Wilcoxon matched-pairs signed-rank test for each species was carried out to examine differences in recruitment (number of recruits per unit area) near and further away from the tree. All analyses were carried out using the statistical software R (version 6.1) (R Development Core Team 2007).

Adult tree species distribution

The GPS locations of individual trees were downloaded as latitude and longitude (degree decimals) and projected to the Universal Transverse Mercator (UTM) 46 N (WGS-84

datum). Nearest neighbour distances for each con-specific was calculated using the package Spatstats (Baddeley & Turner 2005) in R. The measure of spatial dispersion was calculated using the Clark and Evan's (1954) index of clumping for each species. This measure of dispersion accounts for density as well as nearest neighbour distance. The index of clumping ranged from 0 (most clumped) to 2.1491 (most scattered).

The measure of spacing from Clark and Evans (1954) is computed as:

$$\bar{r} = \frac{\sum r}{N}$$

r = the distance in any specified units from a given individual to its nearest neighbour

N = the number of measurements of distance taken in the observed population or sample

\bar{r} = the mean of the series of distances to the nearest neighbour

$\sum r$ = the summations of the measurements of the distance to the nearest neighbour

$$\bar{r}_e = \frac{1}{2\sqrt{\rho}}$$

ρ = the density of the observed distribution expressed as the number of individuals per unit area

\bar{r}_e = the mean distance to the nearest neighbour expected in an infinitely large random distribution of density ρ

$$R = \frac{\bar{r}_a}{\bar{r}_e}$$

R = the measure of the degree to which the observed distribution departs from random expectation with respect to the distance to nearest neighbour

$$\sigma_{r_E} = \frac{0.26136}{\sqrt{N\rho}}$$

σ_{r_E} = the standard error of the mean distance to nearest neighbour in a randomly distributed population of density ρ

RESULTS

Density-dependent effects on seed mortality

Seed removal for all species began from the fourth to sixth day onwards, except for *P. simiarum* and *C. paniculatus* that had little or no removal. In general, the trend for all species at higher seed densities was that of a rapid decline in removal during the initial 20 days. Once few seeds were left, the removal rate declined and was comparable to plots with lower seed densities. The exception was for species such as *D. binectariferum* that showed a rapid decline at high seed densities, but even at lower densities, most seeds were preyed upon immediately (out of 399 seeds that were set out, only 21 seeds were left by Day 20). However some species like *C. paniculatus* and *P. simiarum* showed little or no removal, *P. simiarum* had low seed removal but most mortality was due to rotting (out of 390 seeds set out, 104 rotted).

Daily survival rates consistently decreased with density (LM; $F_{\text{used df}(1), \text{residual df}(92)} = 16.034$, $p < 0.001$) and also varied across species (LM; $F_{\text{used df}(5), \text{residual df}(92)} = 4.4458$, $p < 0.001$). The relationship between daily survival rates and density did not consistently vary across species (LM; interaction term density x species - $F_{\text{used df}(90), \text{residual df}(91)} = 1.4317$, $p = 0.2346$). Except for *C. paniculatus*, all other species showed an increase in mortality with increasing density (Fig. 1).

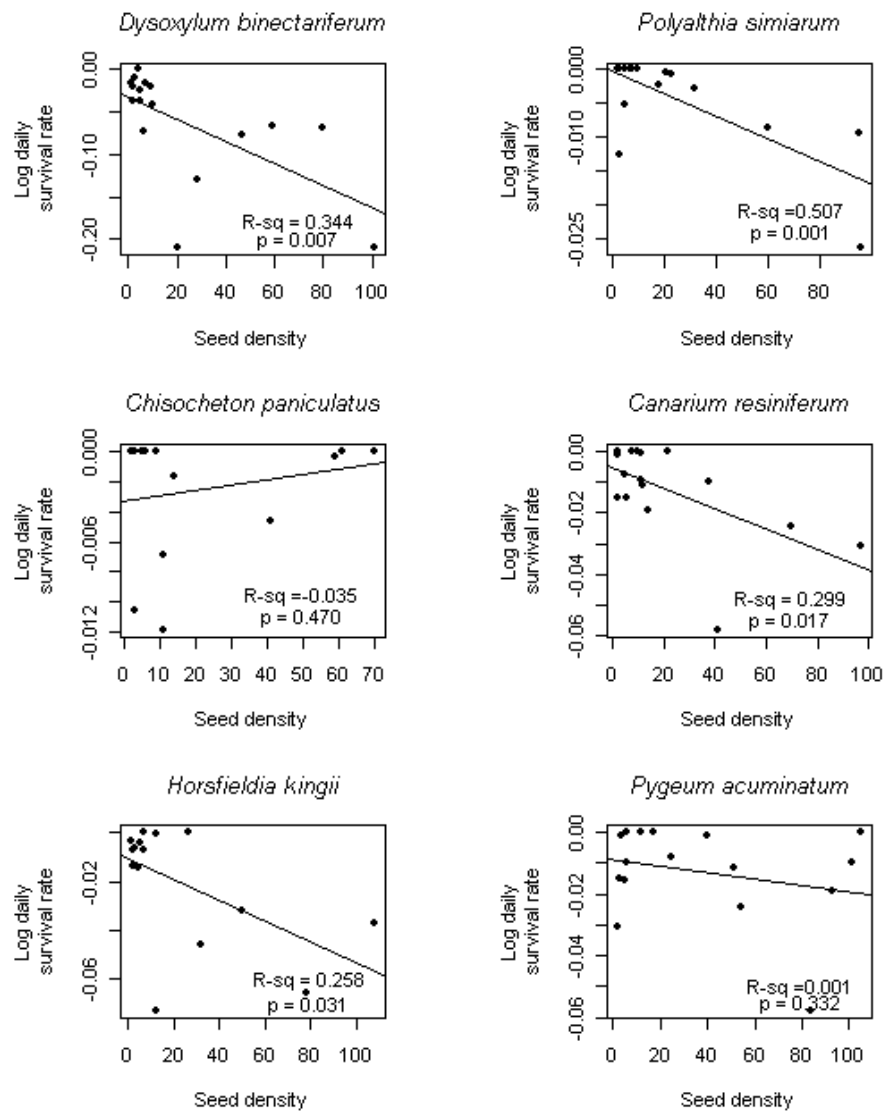


Figure 1. The log of daily survival rate is plotted against density. All species except *Chisocheton paniculatus* show a decline in survival with increasing densities.

Most species show a trend of a decrease in survival with increasing density. When removal rate was quantified, each removal was assumed to be an instance of vertebrate seed predation. However, I found that *P. simiarum* had a high level of beetle larvae infestation which ultimately resulted in rotting at most sites. However, despite lower seed survival due to rotting, *P. simiarum* showed lower mortality (54%) at the seed stage than other species (Table 2). Seed predation alone accounted for only 27% of seed mortality in this species, while for most other species, seed predation levels ranged from 78% - 98% of all seeds.

Table 2. The percentage of seeds preyed across different species. The seeds of *Dysoxylum binectariferum* were the most highly preyed upon, while the seeds of *Chisocheton paniculatus* showed the lowest predation levels. Only the seeds of *Polyalthia simiarum* were recorded to be rotting.

Species	Total seeds	% preyed upon by rodents	% rotten
<i>Chisocheton paniculatus</i>	297	4.1	0
<i>Polyalthia simiarum</i>	390	27.4	26.67
<i>Horsfieldia kingii</i>	349	78.5	0
<i>Canarium resiniferum</i>	351	80.62	0
<i>Pygeum acuminatum</i>	608	92.1	0
<i>Dysoxylum binectariferum</i>	399	98.74	0

Recruitment under parent fruiting trees

Recruitment under parent fruiting trees was variable for each species, with species like *P. simiarum* having as high as 32 recruits for a given tree in the 0 - 2 m interval. The only other species that had recruits near to the parent tree was *C. paniculatus*. *P. simiarum* and *C. paniculatus* were the two species that showed the highest recruitment (mean = 6.05 recruits m⁻² and 1.3 recruits m⁻²) near (0-10 m) the parent tree, species like *C. resiniferum* and *D. binectariferum* also had some amount of recruitment (mean = 0.6 recruits m⁻² and 0.2 recruits

m⁻²) near parent trees. No recruitment was seen for *H. kingii* and *P. acuminatum* near (0 -10 m) to parent trees.

The mean number of recruits as a function of distance and species showed that *C. paniculatus* and *P. simiarum* had a higher number of recruits near the parent tree (Fig. 2). Recruitment varied with distance from the parent tree and the difference in the number of recruits between near and far distance classes varied across species (GLM with Poisson errors; interaction term $\text{distance} \times \text{species}$ Deviance =15.54, $p = 0.008$). There was a significant in the mean densities of recruits between the near and far distance classes from parent trees across species (Kruskal Wallis $H = 42.5939$, $p < 0.01$) (Fig. 3). *C. paniculatus* and *P. simiarum* had greater recruitment near parent trees (Wilcoxon matched-pairs signed-rank test, $Z_{C. \text{paniculatus}} = -3.68$, $p < 0.001$; $Z_{P. \text{simiarum}} = -3.68$, $p < 0.001$), while other species showed similar levels of recruitment near and far from parent trees.

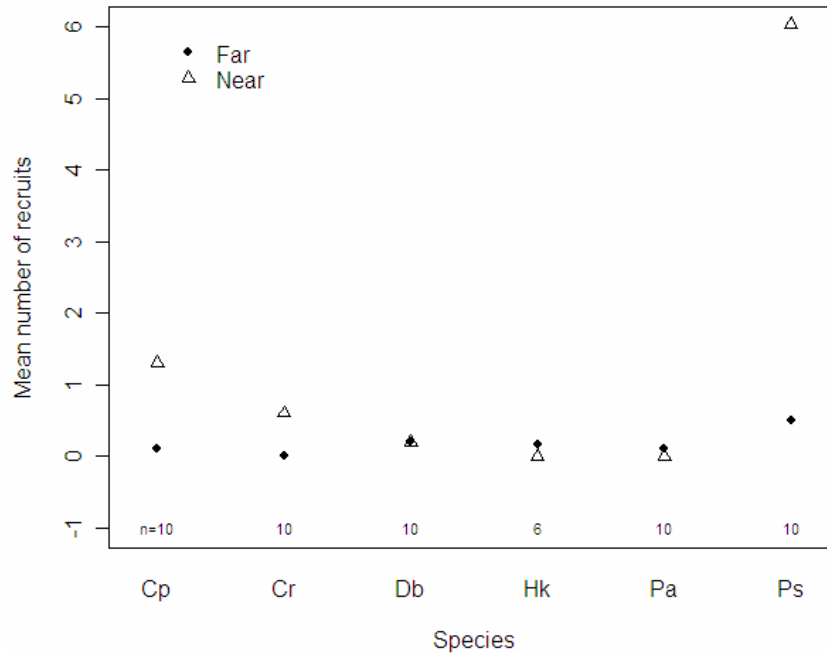


Figure 2. Mean number of recruits at distance classes near (0-10m) and far (10-30 m) under parent fruiting trees for each species (Cp – *C. paniculatus*, Cr – *C. resiniferum*, Db – *D. binectariferum*, Hk – *H. kingii*, Pa – *P. acuminatum*, Ps – *P. simiarum*). *P. simiarum* and *C. paniculatus* showed a higher mean number of recruits near the parent tree, while *D. binectariferum*, *H. kingii*, *C. resiniferum* and *P. acuminatum* showed no differences in the number of recruits near and far.

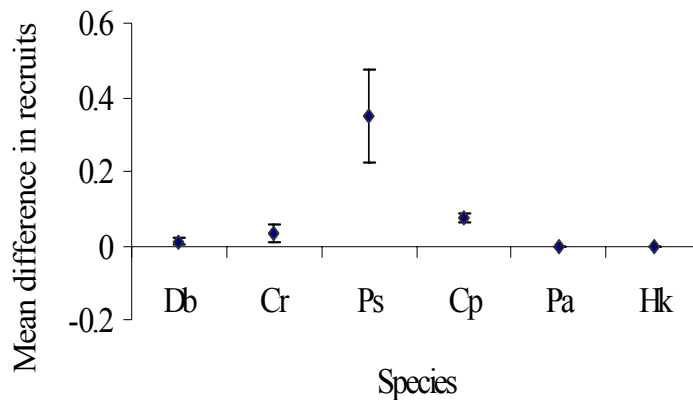


Figure 3. Mean difference in number of recruits near and far for each species (Db – *D. binectariferum*, Cr – *C. resiniferum*, Ps – *P. simiarum*, Cp – *C. paniculatus*, Pa – *P. acuminatum*, Hk – *H. kingii*). N= 10 for each species except *H. kingii* (N=6). Since areas are unequal mean difference for each species is weighted by area for each class near (0-10m) and far (10-30m) and then compared across species. Error bars show standard errors.

Adult tree species density and distribution

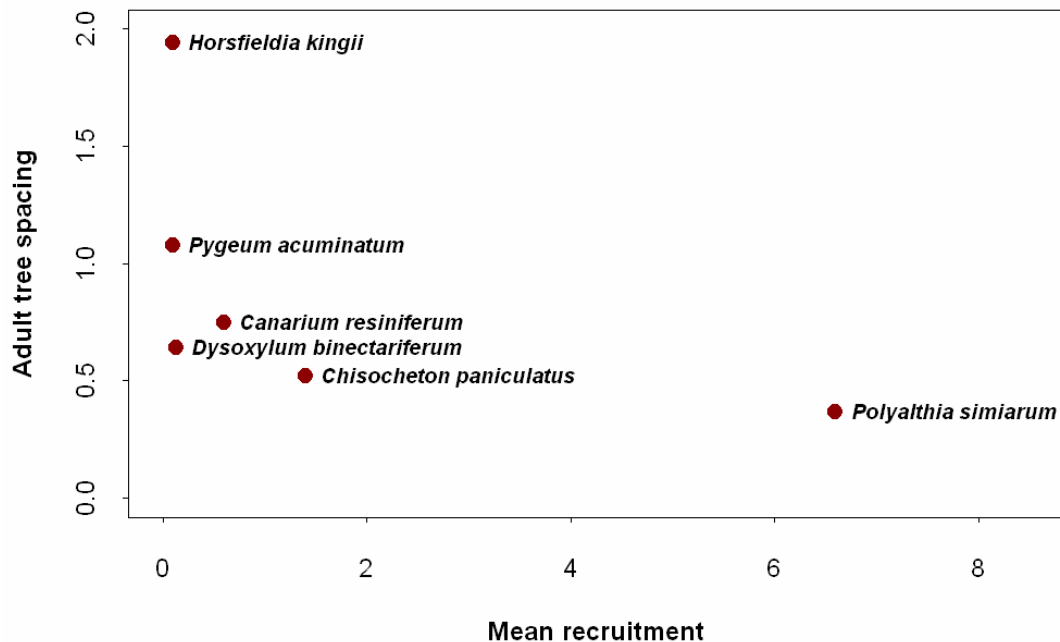
There was variation in nearest neighbour distances between species, with some species with conspecifics located within 10 m from each other, while others were separated by distances greater than 100 m. The mean nearest neighbour distances for common species such as *P. simiarum* ($16.9 \text{ trees ha}^{-1} \pm 0.43_{\text{S.E.}}$) was 4.5 m, whereas the mean distance ranged up to 131 m for *H. kingii*. Though *P. simiarum* had the smallest mean nearest neighbour distance, *C. paniculatus* had the highest densities ($17.82 \text{ trees ha}^{-1} \pm 0.29_{\text{S.E.}}$) with a mean nearest neighbour distance of 6.18 m. *P. acuminatum* and *H. kingii* had the lowest densities ($0.73 \text{ trees ha}^{-1} \pm 1.2_{\text{S.E.}}$ and $0.54 \text{ trees ha}^{-1} \pm 1.22_{\text{S.E.}}$) and the maximum distance between conspecific trees. Using the nearest neighbour and density as a measure of spatial relationships (Clark and Evans 1954), *P. simiarum* was the most aggregated while *H. kingii* had maximum spacing between individuals (Table 3).

Table 3: The Index of spacing in increasing order of scatter, where the value of R ranges from 0 (maximum clumping) to $R = 2.1491$ (maximum spacing of individuals). In the table tree density has been computed as trees/ hectare. However in the analysis of dispersion, both tree densities and mean NND is computed in metres. Across species, *P. simiarum* and *C. paniculatus* are the most clumped and have the highest densities whereas *P. acuminatum* and *H. kingii* are the most scattered with the lowest tree densities.

Species	Mean NND (m)	No of trees hectare ⁻¹	S.E. (trees ha ⁻¹)	Index of dispersion (R)
<i>P. simiarum</i>	4.50	16.90	0.43	0.37
<i>C. paniculatus</i>	6.18	17.82	0.29	0.52
<i>D. binectariferum</i>	15.31	4.36	4.42	0.64
<i>C. resiniferum</i>	15.00	6.18	3.14	0.75
<i>P. acuminatum</i>	63.07	0.73	1.20	1.08
<i>H. kingii</i>	131.35	0.54	1.22	1.94

Establishment, recruitment and adult tree distribution

A Spearman's rank correlation between the percent of seeds preyed upon and the mean recruitment across species (in the 30 m wedge-shape plot across the replicates for each species) showed a negative correlation, but this relationship was not significant ($r_s = -0.609$, $n = 6$, $p = 0.200$). A Spearman's rank correlation between the mean number of recruits and the index of dispersion of each tree species showed a significant negative correlation ($r_s = -0.928$, $n = 6$, $p = 0.008$) (Fig. 4).



DISCUSSION

Seed deposition patterns determine the area of plant recruitment and also set the stage to study processes such as predation (Schupp & Fuentes 1995). Seed predators have the potential to influence patterns of plant recruitment (Edwards & Crawley 1999, Crawley 2000). Studies have shown that seed predators may have different influences with varying seed densities. Several studies have shown seed predation to be independent of seed density,

whereas others have invoked predator satiation when the relationship is inversely dependent, while yet other studies have found seed predation to be directly density dependent (Webb & Willson 1985, Willson & Whelan 1990, Hulme 1994).

High densities of seeds occur under primary deposition sites of hornbill such as nest sites and parent fruiting trees. At nest sites the post-dispersal fate of seeds due predation is an important factor that could potentially re-arrange seed shadows (Chapter 1). In terms of the number of seeds deposited at nest sites, hornbills maybe efficient; however, their quality is severely compromised by the high levels of predation and rotting at these sites.

Seed plots at varying densities showed that all species except *C. paniculatus* showed a negative relationship of survival with density. *P. simiarum* had a high level of beetle larvae infestation which ultimately resulted in rotting at most sites. This could be a reason that it showed a negative trend with increasing density. However, even in the presence of rotting, *P. simiarum* showed lower mortality (54%) at the seed stage than other species.

P. acuminatum showed a negative but weak relationship of survival with density. However 92.1 % of all seeds were preyed upon. Since this species fruits at a period (December-January) where very few other species are available, rodents maybe forced to prey on these seeds.

Density-dependent seed predation could have weakened the link between initial seed densities and consequent plant establishment, but the lack of establishment cannot be solely

attributed to predation. The low proportion of seedlings that emerge from seeds can be explained by seed predation as well as factors such as the intensity of fruiting, pathogen attack, competition between seedlings and limitation of microsites suitable for establishment (Clark *et al.* 2007). The stage between seed production and seedling emergence has been argued to have the strongest demographic filters influencing plant populations (Harper 1977 in Orrock *et al.* 2006). The lack of significance of a negative correlation between the percent seeds preyed on and the mean recruitment across species maybe because of other mortality factors obscuring the effects of predation and an artefact of small sample size ($n = 6$). However species such as *C. paniculatus* and *P. simiarum* exhibit the smallest percent of seeds preyed on and recruitment under parent fruiting trees is higher for these species than for other species. The mean number of recruits under a parent tree was negatively correlated (and significant) with the pattern of spatial dispersion of adult plants measured as clumping or scattering. The species (*C. paniculatus* and *P. simiarum*) that had lower predation showed the highest amount of adult tree aggregation.

Though *D. binectariferum* had the highest mortality risk with increasing density and percent of seeds preyed upon, the measure of adult dispersion showed that it was not the most scattered species. One reason could be that this species is not entirely microsite limited, and when rodents were denied access to these seeds under fruiting trees, these seeds were able to germinate and establish relatively quickly (Chapter 1). Therefore, even if a few seeds escape predation further away from the parent tree, this could result in successful establishment and recruitment.

C. resiniferum shows greater spacing between adult individuals than *D. binectariferum*. Though seed predation by rodents was noted, the stony endocarp of this species may limit the same. Studies on a congeneric species, *Canarium euphyllum* show that seed removal may be mediated by two rare seed-eating rodents, the Indochinese ground squirrel (*Menetes berdmorei*) and the giant long-tailed rat (*Leopoldamys sabanus*) (Kitamura *et al.* 2008). Barking deer (*Muntiacus muntjak*) and sambar (*Cervus unicolor*) are known to consume fruits of this species and deposit the seeds in piles away from the fruiting tree in resting sites (A. Datta, pers. comm.).

P. acuminatum and *H. kingii* experience high levels of seed predation (92.1 % and 78.5 %). Compared to *P. acuminatum* the lower percentage of *H. kingii* seeds preyed upon by rodents could be an artefact of the fewer days these species-plots were monitored. Other results show that *H. kingii* has very high seed predation rates, all seeds marked under parent fruiting trees were preyed upon (n = 100) (Chapter 1). *P. acuminatum* and *H. kingii* have very poor recruitment under parent fruiting trees, and were the two species that have the most spacing between adult individuals.

Studies have shown that seed predation levels often differs among plant species in the same community and can lead to differences in plant species composition (Willson & Whelan 1990; Brown & Heske 1990; Howe & Brown 2000, 2001). The limitation of our study was that recruitment measured under the parent trees was not substantiated with genetic evidence that saplings and seedlings were actually the offspring of nearby adults (Hardesty *et al.* 2006). Based on seed establishment, recruitment under parent fruiting trees and adult tree

distributions, our data show some general trends regarding the life history strategies of the six plant species.

As stated by Howe & Miriti (2004) “The question is no longer whether there is an advantage of escape from the parent but when and where the effect is more important and what is the relative importance of components such as seed and seedling distributions in contributing to structure of communities and populations.”

On a relative scale, for species such *H. kingii*, a rare dioecious tree that is subject to high predation levels under parent fruiting trees, dispersers are likely to be most important for recruitment. For species such as *P. acuminatum*, *D. binectariferum* and *C. resiniferum* that have high predation levels, low recruitment under parent fruiting trees, and well spaced adult tree distributions, primary dispersers maybe important in aiding escape and colonization to new sites. For species such as *C. paniculatus* and *P. simiarum* that have low predation levels, high recruitment under parent fruiting trees, and aggregated adult tree distributions, dispersers maybe relatively unimportant for recruitment and survival, however may be needed to enable colonization of new sites in space and time.

Our work is the first step in trying to understand how seed predators can shape the distribution of plants communities at a relatively large scale. Our study suggests that species differ in their ability to withstand density-dependent mortality and this has consequences for establishment and adult tree densities and distributions. Some species that are not dispersal-limited such as *C. paniculatus* and *P. simiarum* may therefore be able to recruit in the

absence of dispersers. *P. simiarum* is also known to have a wider range of consumers and dispersers. Such species are likely to suffer fewer consequences if their dispersers decline in abundance or become locally extinct. Species that show high density dependent mortality at parent trees are likely to have poor regeneration in the absence of their primary dispersers. In addition, sites, where large vertebrate dispersers disappear due to hunting, abundances of rodents may often increase as they are often not specifically targeted by hunters (Corlett 1996). This would have greater negative consequences for species that are vulnerable to seed predation. Where plant-animal interactions are disrupted due to anthropogenic disturbances, in the long-term, relative abundance and distribution patterns of plant communities may be affected resulting in dominance of species with life-history strategies that are able to cope with lack of dispersal (Wright *et al.* 2007, Muller-Landau 2007).

ACKNOWLEDGEMENTS

This work was mainly funded by the Wildlife Conservation Society, USA. I thank the Nature Conservation Foundation, Mysore, for logistic support and financial help. I also wish to thank the Arunachal Pradesh Forest Department for granting permission and facilitating the fieldwork. Kumar Thappa, Tagge Talang, Rajan Bahadur, Rasham Barra and Narayan Mogar made this work possible with their immense support in the field. I thank Suhel Quader and Ajith Kumar for help in data analyses.

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CONCLUSION

A high percentage of plant species in tropical forests are animal-dispersed. Research on the interactions between plants and their vertebrate dispersers is important to understand the consequences of seed dispersal in determining plant recruitment patterns. The results of this study show that rodents are mainly seed predators and not secondary seed dispersers in the study area. There are differential predation levels across species which has consequences for establishment. Further some species show no difference in survival in the presence or absence of rodents. Nest sites of hornbills where seeds are deposited in clumps have greater per capita seed mortality compared to fruiting trees because of predation and additional density dependent-mortality related to rotting. I also found that species differ in their ability to withstand density-dependent mortality and this has consequences for establishment and adult tree densities and distributions. Species such as *Chisocheton paniculatus* and *Polyalthia simiarum* had lower predation levels, greater recruitment near parent trees, showed the highest amount of aggregation as adult trees and had higher abundance. Highly preyed upon species such as *Horsfieldia kingii*, showed very little recruitment under parent fruiting trees and maximum spacing among adult trees and was rare. A key unanswered question that remains is why some species have evolved strategies to cope with density-dependence, while others do not, given that all the ones are under study are dispersed in both scatter and clumped manner. This study underlines the effects that rodents have on plant communities of different plant species. It also highlights the fact that tree species vary in their response to density-dependence mortality factors such as predation, which suggests that some species are able to recruit and establish in the absence of dispersers, while others may require primary dispersers such as hornbills to escape predation at high seed densities. In addition,

particularly in South-east Asia where large vertebrate dispersers have disappeared due to hunting, this would have greater negative consequences for plant species that are vulnerable to seed predation.