

Effect of rodents on seed fate of five hornbill-dispersed tree species in a tropical forest in north-east India

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(Accepted 27 May 2009)

Abstract: Hornbills are important dispersers of a wide range of tree species. Many of these species bear fruits with large, lipid-rich seeds that could attract terrestrial rodents. Rodents have multiple effects on seed fates, many of which remain poorly understood in the Palaeotropics. The role of terrestrial rodents was investigated by tracking seed fate of five hornbill-dispersed tree species in a tropical forest in north-east India. Seeds were marked inside and outside of exclosures below 6–12 parent fruiting trees (undispersed seed rain) and six hornbill nest trees (a post-dispersal site). Rodent visitors and seed removal were monitored using camera traps. Our findings suggest that several rodent species, especially two species of porcupine were major on-site seed predators. Scatter-hoarding was rare (1.4%). Seeds at hornbill nest trees had lower survival compared with parent fruiting trees, indicating that clumped dispersal by hornbills may not necessarily improve seed survival. Seed survival in the presence and absence of rodents varied with tree species. Some species (e.g. *Polyalthia simiarum*) showed no difference, others (e.g. *Dysoxylum binectariferum*) experienced up to a 64% decrease in survival in the presence of rodents. The differing magnitude of seed predation by rodents can have significant consequences at the seed establishment stage.

Key Words: *Chisocheton cumingianus*, *Dysoxylum binectariferum*, hornbills, *Horsfieldia kingii*, *Polyalthia simiarum*, *Prunus ceylanica*, 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, therefore, have effects on subsequent life-history stages, such as seed establishment and seedling recruitment (Wenny 2001). Hornbills are important, well-studied seed dispersers of many tree species in African and Asian tropical forests (Datta 2001, Kinnaird 1998, Kitamura *et al.* 2004a, 2004b; Whitney *et al.* 1998). They are known to forage on a variety of fruit resources, from small-sized sugar-rich fruits to large lipid-rich fruits (Datta & Rawat 2003). Seeds of many of these fruits are medium- to large-sized and lipid-rich which makes them attractive for rodent consumption.

Rodents are an important group that impacts seed fate through multiple processes (Forget 1996, Forget *et al.* 2002). Studies in the Neotropics have shown that rodents can either limit establishment through seed predation (Wenny 2000) or enhance germination through multiple mechanisms. These include the scatter-hoarding and subsequent non-recovery of caches (Jansen *et al.* 2004) and the decrease of density-dependent seed mortality, mediated via predation (Forget *et al.* 1999, 2002; Pizo 1997, Wenny 1999). Scatter-hoarding can also result in enhanced germination by directed dispersal to suitable microsites such as patchily distributed canopy gaps (Jansen & Forget 2001).

In the Palaeotropics, the effect of rodents on seed fate has been little studied. However, there is some evidence for scatter-hoarding (e.g. species belonging to the genus *Leopoldamys*; Cheng *et al.* 2005, Kitamura *et al.* 2008, van der Meer *et al.* 2008, Xiao *et al.* 2004, Yasuda *et al.* 2000, 2005; Zhang *et al.* 2008) and for seed predation (e.g. by *Hystrix brachyura* Linn., *Niviventer*

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Table 1. Fruit and seed characteristics of five hornbill-dispersed tree species selected for the study. Sources: Datta (2001), Datta & Rawat (2003).

Tree species	Family	Fruit type	Fruiting period	Seed weight (g)	Seed size (mm)	
					Length	Width
<i>Chisocheton cumingianus</i> C. DC.	Meliaceae	Lipid-rich arillate capsule	April–July	7.99	31.7	23.9
<i>Dysoxylum binectariferum</i> Roxb.	Meliaceae	Lipid-rich arillate capsule	February–May	6.65	32.3	24.6
<i>Horsfieldia kingii</i> Warb.	Myristicaceae	Lipid-rich arillate capsule	February–May	7.84	35.7	20.2
<i>Polyalthia simiarum</i> Benth. & Hook.	Annonaceae	Lipid-rich drupaceous carpel	December–February; May–July	1.82	20.2	12.3
<i>Prunus ceylanica</i> (Wight) Miq.	Rosaceae	Single-seeded drupe	November–February	4.30	20.6	15.1

sp. and *Rattus* sp.; Cheng *et al.* 2005, Kitamura *et al.* 2004a).

We examined the effects of rodents on seed fates of five tree species that are dispersed by hornbills, in a tropical forest in north-east India. We focused on species with large, lipid-rich seeds, traits likely to attract rodents. The effects that rodents have on seeds of these species could operate at parent fruiting trees and also at post-dispersal sites, such as hornbill nest trees. At hornbill nest trees, seeds of different species accumulate over the long breeding season and are likely to attract seed predators (such as terrestrial rodents). At these sites, seeds may also experience additional mortality due to interspecific competition. At parent fruiting trees of these large-seeded species, seed rain is dominated by a single species and apart from seed predation, mortality is due to host-specific pathogens (Packer & Clay 2000).

We examined variation in rodent effects across tree species and across different types of seed deposition sites. We assessed seed fate of the five different tree species in the presence and absence of rodents at parent fruiting trees (where seeds fall undispersed) and hornbill nest trees where post-dispersal effects operate. Seed removal and/or predation and other mortality factors are expected to be higher at post-dispersal sites such as at hornbill nest trees (where seeds of many species are deposited together, accumulate over several months, and attract rodents). We discuss the consequences of these findings for plant recruitment and establishment.

STUDY SITE AND SPECIES

The study was carried out from December 2007 to May 2008 in the tropical foothill forests of western Arunachal Pradesh in Pakke Wildlife Sanctuary and Tiger Reserve (92°36'–93°09' E; 26°54'–27°16' N; 862 km²). The terrain is undulating and hilly with an altitudinal range of 150–1500 m asl (Datta 2001). Pakke has a tropical and subtropical climate with a cool season 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 1968). A total of 343 woody species of angiosperm have been recorded, but at least 1500 vascular plants are likely to occur (Datta 2001, Datta & Rawat 2003). The intensive study area (c. 9 km²; 150–220 m asl) was located in the south-eastern part of the sanctuary. The most common hornbill-dispersed tree species are *Polyalthia simiarum*, *Chisocheton cumingianus* and *Aglaia spectabilis* (Miq.) Jain & Bennet.

The important avian frugivores in the area are three species of hornbill: great hornbill (*Buceros bicornis* Linn.), wreathed hornbill (*Aceros undulatus* Shaw) and Oriental pied hornbill (*Anthracoceros albirostris* Shaw & Nodder). There are about 45–50 frugivorous bird species in this area (Datta & Rawat 2008). Thirteen species of green pigeon, parakeet and dove occur here; however, they are mainly seed predators (Lambert 1989, Walker 2007).

The pre-dispersal seed predators found here include four species of diurnal tree squirrel (Himalayan striped squirrel *Tamiops maccllellandi* Horsfield, hoary-bellied squirrel *Callosciurus pygerythrus* Hilaire, Pallas red-bellied squirrel *Callosciurus erythraeus* Pallas and the Malayan giant squirrel *Ratufa bicolor* Sparmann). Among the terrestrial rodent species known to occur in the area, the Himalayan crestless porcupine *Hystrix brachyura*, brush-tailed porcupine *Atherurus macrourus* Linn., Himalayan rat *Rattus nitidus* Hodgson, Norway rat *Rattus norvegicus* Berkenhout, *Bandicota* spp. and *Niviventer* spp. are reported to prey on seeds, while Edwards's long-tailed rat *Leopoldamys edwardsi* has been reported to scatter-hoard seeds (Cheng *et al.* 2005, Zhang *et al.* 2008).

The five (non-fig) tree species selected for this study (Table 1) are among the most important species in the diet of hornbills in the area (Datta 2001, Datta & Rawat 2003) and some are known to be preyed upon by rodents (Datta 2001). All the selected tree species were medium to large-seeded (>2 cm) with lipid-rich fruits (Table 1). *Prunus ceylanica* was fruiting from December to January. Fruiting of *Dysoxylum binectariferum*, *Chisocheton cumingianus* 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.

METHODS

Seed fate: parent trees and hornbill nest trees

We monitored seed fate below parent trees of five study tree species by establishing rodent-proof metal exclosures (1 m × 1 m, height 1.4 m) below 6–12 parent fruiting trees of each of the five selected tree 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 12 km to the north-west of the intensive study site. Exclosures for each species were set up at different times, as and when individual trees fruited. Seeds were handled using latex gloves to avoid leaving a scent of any kind. Ten seeds were placed inside each metal exclosure, and ten seeds were placed in an adjacent plot of the same size left open to rodents. Seeds left open to rodents were individually marked with coloured fishing line (diameter 0.5 mm, 40 cm in length) using non-toxic glue (Loctite® Super Glue Ultra Gel™), while seeds inside the exclosures were not marked. The marked seeds were allowed to dry and the attachments were re-checked. Similar marking techniques have been used in the Neotropics with no evidence of effects on seed removal (Forget 1996).

We also examined seed fate at nest sites of hornbills (post-dispersal sites). Hornbills regurgitate and deposit seeds of several species below nest trees during the breeding season (March–July). Fruits of *Polyalthia simiarum*, *Horsfieldia kingii*, *Chisocheton cumingianus* and *Dysoxylum binectariferum* ripen and are consumed by hornbills during the early part of the breeding season (March–May), which coincided with our study period. Twenty seeds of each of these four tree species were placed inside and outside exclosures below two nest trees of the great hornbill and four of the wreathed hornbill. As seed densities were higher at nest trees, we set out a higher number of seeds than that below parent trees. Our assessment of seed fate below nest trees was restricted to experiments with seeds of a single species at a time. The seeds were placed 2.5 m away from the base of the nest tree in separate exclosures for each species. All nest trees were of *Tetrameles nudiflora* Roxb. (an emergent wind-dispersed species).

Tracking seed fate

The fate of marked seeds in the plots outside exclosures (i.e. eaten, cached, rotten, intact uneaten and germinated) was monitored every 3 d. For each species (at parent and nest trees), the fate of individual seeds was tracked for as long as seeds remained in the plot open to rodents or if

cached, until the cached seed germinated or was eaten. Such tracking of seed fate was done either until all seeds were preyed upon/disappeared in a plot or until the end of the study, whichever occurred earlier. Therefore, seeds were monitored for a variable length of time depending on fruiting period and fate of seeds. Seed fate was tracked for a minimum of 45 d (for species such as *C. cumingianus* that fruited later during the study) to a maximum of 108 d (for earlier fruiting species such as *P. ceylanica*). 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. Seed mortality due to other factors, such as pathogen or fungal attack, was also noted. The remaining seeds were monitored until establishment, which was defined as the emergence of cotyledons. Seeds that were cached were also monitored to determine various seed fates: retrieved and eaten, not retrieved and germinated, not retrieved and viable, not retrieved and dead.

The fate of unmarked seeds placed inside exclosures was also monitored until the establishment stage or the end of the study, whichever occurred earlier (the duration of monitoring ranged from 45 to 108 d). The main fates of seeds inside exclosures were germinated, viable and non-viable. At the end of the study, seeds that remained (both inside exclosures and in the unprotected plots) were examined and classified as hollow, solid or infested by insects. The viability of solid seeds was ascertained using the tetrazolium dye test (Malone 1967). At the end of the study, the number of seeds that were viable and non-viable was ascertained.

Monitoring seed removal by rodents with camera traps

In addition to the 500 and 480 seeds that were marked and left open to rodents at parent fruiting trees and nest trees, we also marked 410 seeds for our camera trapping study. We used three camera traps in order to establish the identity of rodent visitors and determine how they handled seeds. The equipment consisted of a digital camera (Olympus D 380, 35 mm with 2 megapixel resolution) placed in a weatherproof box with a passive infra-red detector (manufactured by the Centre for Electronics Design and Technology, Indian Institute of Science, Bangalore). The camera traps were set up to take four pictures min^{-1} when an animal passed in front of the sensor with a minimum delay of 15 s. The time and date were set and the camera operated continuously for 24 h. Three camera traps were set up below three parent 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 20 d.

Seeds were replenished as and when they were removed or eaten up. If seeds were cached, their fate was tracked until 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 <http://www.R-project.org>).

To examine variation in seed viability in the presence and absence of rodents (exclosure experiments), we first calculated the difference in the proportion of seeds viable inside each exclosure and outside in the adjacent paired plot (Inside–Outside). We used this difference as our measure of the effect of rodents on seed viability. We examined whether the effect of rodents on seed viability varied among the five tree species and between parent fruiting and nest trees, using a linear model with normal errors. The difference in proportion viable was the response variable (each exclosure–adjacent plot pair provided an independent data point), and the explanatory variables were tree species, tree type (nest/parent tree) and monitoring time (included to incorporate the potential effects of variable sampling period). For factors identified as significant in the linear model, post hoc multiple comparison tests (Tukey's Honestly Significant Difference Test) were used to examine differences between factor levels. The interaction between the two explanatory variables was not significant ($P > 0.2$) and was not included in the final model. Similarly, monitoring time was not significant ($P > 0.2$) and therefore not included in the final model. We checked residuals for deviation from model assumptions. To assess separately at each tree type for each species whether seed viability differed inside and outside exclosures, we examined whether 95% confidence intervals of the difference in proportion viable included 0, i.e. no difference.

RESULTS

General patterns in seed fate

Across all tree species, out of the 1390 seeds marked, only 20 seeds of three species were cached (*Dysoxylum binectariferum*, *Polyalthia simiarum* and *Prunus ceylanica*). Of these, only three seeds of a single species (*P. ceylanica*) germinated. All other cached seeds were retrieved and eaten. Seed predation was a primary cause of seed mortality; 73.2% of all marked seeds were preyed upon on-site. Overall, seed mortality was high: 92% of seeds at nest trees and 74.6% at parent trees.

In addition to predation, rotting was the other main cause of seed mortality. Levels of rotting were substantially higher at nest trees than at parent fruiting

trees; as a result, although the percentage of seeds preyed upon was lower at nest trees (51.5%) than at parent trees (57.8%), overall mortality was greater at nest trees.

A total of 980 seeds were set out within exclosures, 500 at parent fruiting trees and 480 at nest trees. Rotting was the cause of seed mortality inside exclosures (Figure 1).

Across species, 54.4% of seeds at parent fruiting trees and 28.7% at nest trees survived inside exclosures. *Prunus ceylanica* had the highest percentage of seeds viable inside exclosures (70%) while *H. kingii* had the lowest (25%).

Comparison among tree species

Rodents had differential effects on seed fates of the study species. *Chisocheton cumingianus* and *P. simiarum* showed the lowest predation (1.9% and 16.9% respectively; data pooled across parent and nest trees) (Table 2).

For species heavily preyed upon such as *D. binectariferum* and *H. kingii*, there was a reduction of viability by 64% and 25% respectively at parent trees in the presence of rodents. At nest trees, only *D. binectariferum* showed a difference in viability inside and outside rodent exclosures (Figure 2).

On assessing these patterns formally, in the linear model with tree species and tree type, tree species explained substantial variation in the difference in proportion viable inside and outside exclosures ($F_{3,59} = 53.5$; $P < 0.001$; change in R^2 when removed from model = 72.5%). Post hoc comparisons showed differences between *D. binectariferum* and *C. cumingianus*, *D. binectariferum* and *P. simiarum*, *H. kingii* and *P. simiarum* (Table 3).

Comparison between parent and nest trees

The influence of rodents on seed viability did not differ significantly between parent and nest trees. In the linear model with tree species and tree type, tree type explained little variation in the difference in proportion of seeds viable inside and outside exclosures ($F_{1,59} = 0.61$; $P = 0.54$; change in R^2 when removed from model = 0.18%).

Camera traps and rodent visitors

Camera-trap monitoring showed that all seeds of *D. binectariferum*, *H. kingii* and *P. ceylanica* were consumed on-site. For these species, rodent visitation rates were high. The Himalayan crestless porcupine and the brush-tailed porcupine were the major predators and most frequent visitors (Table 4). These two species preyed on seeds directly on-site. A small proportion of seeds of *P. simiarum* were preyed upon only by a *Niviventer* sp. No vertebrate was seen consuming seeds of *C. cumingianus*.

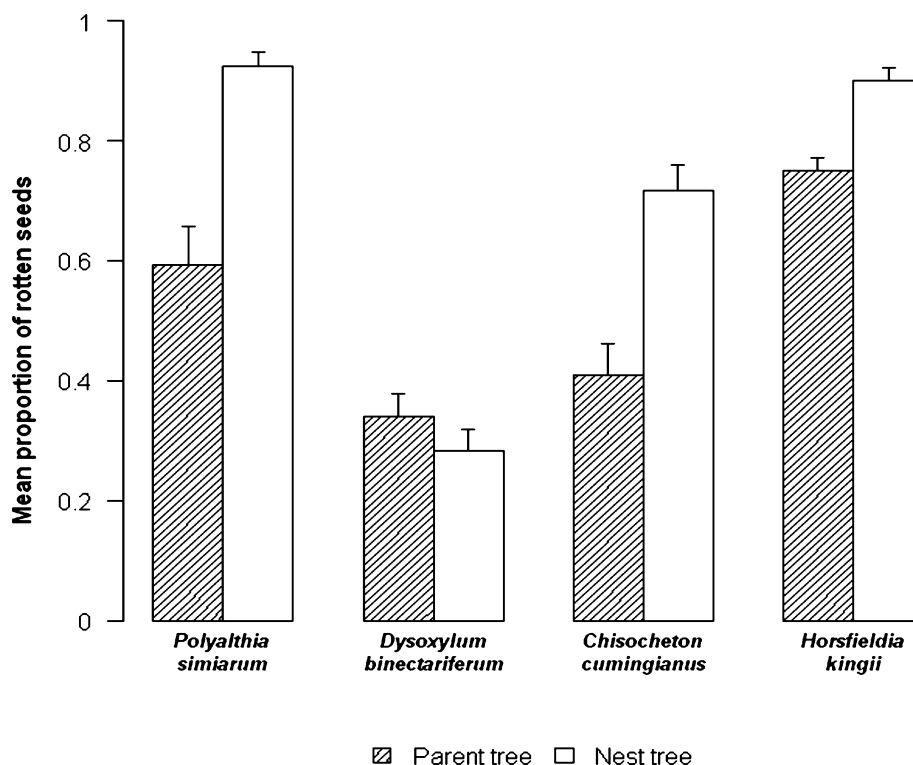


Figure 1. Mean proportion of rotten seeds inside exclosures below parent trees and hornbill nest trees. Error bars indicate SE.

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

DISCUSSION

Hornbills are important seed dispersers of nearly one-quarter of the tree species recorded from Pakke Tiger Reserve (Datta & Rawat 2008). We found that rodents had differential effects on seed survival of the five study species (selected from the important plant families in the diet of hornbills). There was also relatively higher predation at hornbill nest sites. Terrestrial rodents were mainly seed predators of large-seeded hornbill-dispersed tree species.

Caching, which could result in effective dispersal through non-retrieval of caches, was uncommon (only 1.43% were cached, most of which were subsequently retrieved and eaten).

Other studies in the Palaeotropics have also found little evidence of rodents behaving as seed dispersers (Cheng *et al.* 2005, Yasuda *et al.* 2000, 2005), in contrast to Neotropical patterns of high caching and enhanced plant establishment (Jansen & Forget 2001). In the Neotropics, seeds of many large-seeded tree species are scatter-hoarded, often up to 70% of seeds in some species (Forget 1990). The greater degree of caching by rodents at Neotropical sites may be related to the comparatively greater seasonal variation in resource availability, where seeds are cached during the resource-rich wet season (Forget 1990, Forget *et al.* 2002). In Pakke, although there is seasonal variation in fruiting with a lean fruiting period (August–January), species

Table 2. The various fates of marked seeds of five tree species in the plots open to rodents and at camera traps (n = 1390). The data have been summarized as the per cent of seeds that have different fates. For each species, the data have been pooled across parent and hornbill nest trees and camera traps, except for *Prunus ceylanica* where data are only from parent trees and camera traps. N represents the number of seeds set out for each of the tree species.

Species (N)	Eaten	Cached	Germinated	Lost	Rotten	Intact uneaten
<i>Chisocheton cumingianus</i> (250)	1.9	0	0	0.6	38.7	58.7
<i>Dysoxylum binectariferum</i> (350)	97.7	2.29	0	0	0	0
<i>Horsfieldia kingii</i> (280)	96.2	0	0	0	1.9	1.9
<i>Polyalthia simiarum</i> (280)	16.9	1.7	0.02	3.4	50.9	27.5
<i>Prunus ceylanica</i> (230)	78	5.3	2.8	4	2.7	7.2

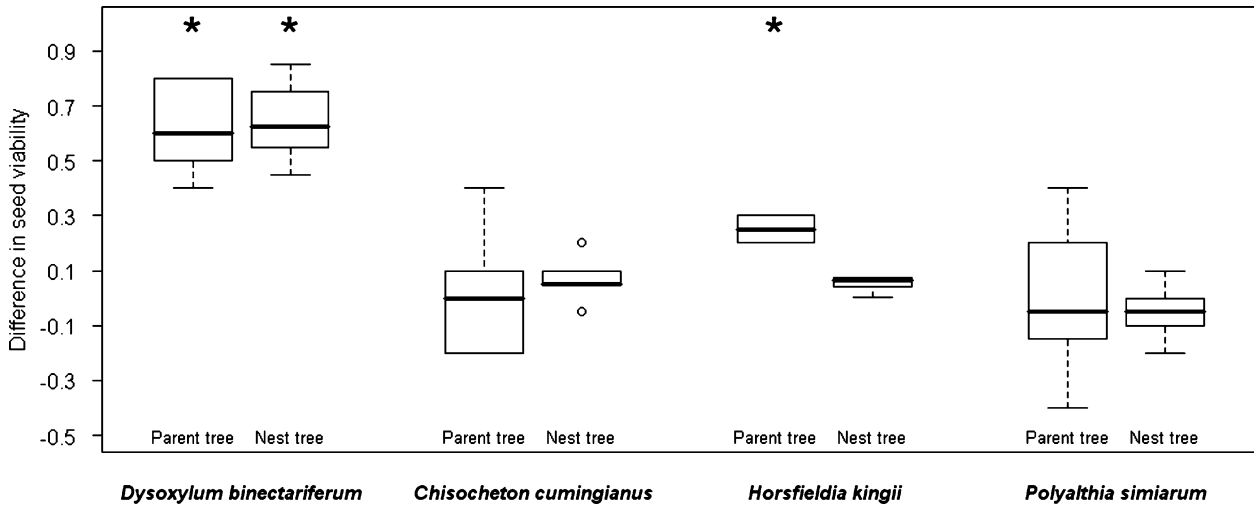


Figure 2. Difference in proportion of seeds that were viable inside and outside exclosures at parent and hornbill nest trees for four tree species. The box plot represents the 1st and 3rd quartile with the median, while the whiskers represent the range of data from the smallest to the largest value. Confidence intervals of the difference in proportion viable that do not include zero, i.e. a statistically significant difference in viability, are indicated as *.

such as *P. simiarum*, *P. ceylanica* and several tree species belonging to the family Lauraceae (*Actinodaphne*, *Alseodaphne*, *Beilschmiedia*, *Litsea*) continue to fruit during this period (Datta 2001). The lack of caching could be also because this study coincided with the relatively resource-rich period (January–May) and a longer study may be needed to conclusively understand seasonal and annual variations in caching behaviour (Forget *et al.* 2002).

Camera-trap monitoring showed that the dominant seed predators were large-bodied rodents (Himalayan crestless porcupine and brush-tailed porcupine) that are unlikely to scatter-hoard seeds (Kitamura *et al.* 2004a,

Yasuda *et al.* 2005). These two species appear to be very common in the area based on visitation rates at camera traps (this study) and relative abundance estimates from a previous study (A. Datta, unpubl. data). The other rodent visitors (*Berylmus* sp., *Niviventer* sp. and *Rattus* sp.) are not known to cache seeds (Cheng *et al.* 2005), while *Callosciurus pygerythrus* is primarily an arboreal seed predator. *Leopoldamys edwardsi* is the only rodent species from Asia that is known to cache seeds (Cheng *et al.* 2005, Yasuda *et al.* 2000, 2005; Zhang *et al.* 2008). Distribution records suggest that this species may occur in our study area although we did not record its presence. The identity

Table 3. Post hoc pairwise comparisons between tree species of the difference in proportion viable inside and outside exclosures at parent and hornbill nest trees (Tukey’s Honestly Significant Difference Test). Difference = Species 1 (Proportion viable inside – outside) minus Species 2 (Proportion viable inside – outside). 95% confidence intervals of the difference between species are shown.

Species pair	Difference	95% CI of difference	P
<i>Chisocheton cumingianus</i> – <i>Dysoxylum binectariferum</i>	0.60	0.44 to 0.75	< 0.01
<i>Chisocheton cumingianus</i> – <i>Horsfieldia kingii</i>	0.12	–0.05 to 0.29	0.26
<i>Chisocheton cumingianus</i> – <i>Polyalthia simiarum</i>	–0.05	–0.20 to 0.11	0.85
<i>Dysoxylum binectariferum</i> – <i>Horsfieldia kingii</i>	–0.48	–0.65 to –0.31	< 0.01
<i>Dysoxylum binectariferum</i> – <i>Polyalthia simiarum</i>	–0.65	–0.80 to –0.50	< 0.01
<i>Horsfieldia kingii</i> – <i>Polyalthia simiarum</i>	–0.17	–0.34 to 0.00	0.05

Table 4. Rodent visitation rates and percentage of seed predation based on camera trapping. Seeds were placed below three individual trees of each of the five tree species. Trapping effort was 60 d of trapping per species totalling 300 d.

Tree species (n)	Visitation rates (visitors d ⁻¹)	Total percentage of seeds preyed upon	Per cent eaten by single species	Species that consumed most seeds
<i>Chisocheton cumingianus</i> (30)	0	0	0	-
<i>Dysoxylum binectariferum</i> (110)	0.75	100	77	Himalayan crestless porcupine
<i>Horsfieldia kingii</i> (100)	0.53	100	82	Brush-tailed porcupine
<i>Polyalthia simiarum</i> (40)	0.2	25	25	<i>Niviventer</i> sp.
<i>Prunus ceylanica</i> (130)	0.8	100	33	Brush-tailed porcupine

of rodent species that cache seeds in the area remains unknown.

The magnitude of seed predation by rodents varied among the tree species that we studied. While *C. cumingianus* and *P. simiarum* were preyed upon much less by rodents, *D. binectariferum*, *P. ceylanica* and *H. kingii* were heavily preyed upon. For species such as *D. binectariferum*, *H. kingii* and *P. ceylanica*, predation reduced seed viability by 25% to more than 50%. For these species (more than 80% of seeds were consumed), rodents are likely to have a negative effect by limiting seed establishment.

Seed deposition by hornbills is aggregated at nest trees and similar to the high density conditions below parent fruiting crowns (Datta 2001). Hornbill nest trees have been considered important foci for seed dispersal and recruitment (Kinnaird 1998, Whitney *et al.* 1998) but we found that they were not particularly suitable for seed establishment and recruitment (see also Kitamura *et al.* 2004c). The high seed densities at nest trees appear to lead to density-dependent mortality due to seed predation and rotting, especially in the absence of caching which would have positive effects by decreasing density-dependent effects on seed survival. However, mortality factors at nest trees differ from those at parent fruiting trees. Density-dependent mortality at parent trees would be driven by intraspecific competition and host-specific pathogens (Packer & Clay 2000), while at nest trees, mortality would be largely due to interspecific competition and rodent species-specific seed preferences.

To conclude, rodents were seed predators of the large-seeded hornbill-dispersed tree species and did not act as seed dispersers. Interestingly, we found that the magnitude of seed predation by rodents differed across the five tree species we studied. The variation in seed survival has consequences for seedling recruitment and plant establishment. Seeds of species that have low predation would be expected to have higher recruitment compared with species that have high levels of seed predation. Such species are likely to be less affected by density-dependent mortality due to predation and are expected to recruit better than species that are affected by density-dependent predation, contrary to the predictions of the Janzen–Connell hypothesis (Connell 1971, Janzen 1970). This study highlights the effects of rodents on the establishment stage and hence on later life-history stages of forest tree communities.

ACKNOWLEDGEMENTS

This work was funded by the Wildlife Conservation Society, India Programme. We thank the Nature Conservation Foundation, Mysore and the Centre for Electronics Design and Technology, Indian Institute of Science, Bangalore for logistic support and providing

equipment. The Arunachal Pradesh Forest Department granted permission and facilitated fieldwork. Kumar Thapa, Kishore Dorje, Tagge Talang, Rajan Bahadur, Rasham Barra and Narayan Mogar made this work possible with their immense support in the field. Suhel Quader and Ajith Kumar helped with data analyses and provided valuable comments. We thank M.S. Pradhan for help with rodent identification. We thank P.A. Jansen and two anonymous reviewers for valuable comments on this manuscript.

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