TECHNICAL REPORT

CONSEQUENCES OF HORNBILL DECLINES FOR SEED DISPERSAL AND TROPICAL TREE REGENERATION IN THE INDIAN EASTERN HIMALAYAS

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CONTENTS

1. SUMMARY

The study indicted that mean abundances of the Great (*Buceros bicornis*), the Wreathed (*Aceros undulatus*) and the Oriental Pied Hornbills (*Anthracoceros albirostris*) were 96.7%, 83.1% and 71.9% lower in hunted than in protected forests. Conversely, the Mountain Imperial Pigeon (*Ducula badia*), which is not actively targeted by hunters in our forests showed an increasing trend in hunted sites although abundances were not significantly different between sites. Declining hornbill populations were mirrored in the recruitment patterns of large-seeded tree species; four large-seeded tree species, *Amoora wallichii*, *Chisocheton paniculatus*, *Dysoxylum binectariferum* (All Meliaceae) and *Polyalthia simiarum* (Anonaceae) showed severely depressed recruitment of seedlings, juveniles and saplings in hunted sites as compared with protected forests. Visitation rates and seed removal patterns indicate that hornbills and *Ducula* pigeons are the only dispersers for the capsular, arillate, meliaceae species. Although *Polyalthia* has a much larger disperser assemblage than the other large-seeded trees, it too appears to be recruitment limited in hunted sites. Hornbills may also be important dispersers of some but not all of the smaller-seeded tree species. A small-seeded drupaceous tree, *Cinnamomum bejolghota* (Lauraceae) relied heavily on small and medium bodied birds for its dispersal but not hornbills, while another smaller-seeded tree, *Actinodaphne obovata* was not recruit limited at hunted sites, possibly because of it large disperser assemblage. These results indicate that declining hornbill populations adversely impacts the dispersal and recruitment of large-seeded tree species and conservation measures need to focus on reducing hunting pressures but also widespread logging and habitat degradation that are increasingly afflicting the foothill forests of Arunachal.

2. INTRODUCTION

Hunting of frugivorous species is widespread in tropical forests with potentially adverse consequences for plant-animal interactions and forest dynamics (Redford, 1992, Peres 2001). Frugivorous animals by moving seeds to favorable microsites for establishment (Wenny and Levey, 1998, Wenny, 2001), helping them 'escape' from zones of density and distance-dependent mortality in the vicinity of parent plants or colonize new habitats have been shown to confer critical survival benefits thereby playing an integral role in tree recruitment (Schupp 1988, Terborgh et al. 1993, Howe et al. 1985, Howe, 1990) and ecological restoration. Because most tropical trees bear fruits that are animal dispersed, the loss of critical seed dispersers may ramify through the ecosystem with profound effects on seedling demography and spatial ecology (Chapman and Chapman, 1995, Harms et al 2000) through severed mutualisms with tropical trees (Cordeiro and Howe, 2003) and hampered plant recruitment (Howe, 1993). In the Indian Eastern Himalayas, intensive hunting of hornbill dispersers by local tribes for meat and ornamentation is predicted to have significant, though largely unquantified consequences for forest regeneration and diversity.

In this study, I test whether tribal hunting of hornbills in the Eastern Himalayas adversely impacts the dispersal and regeneration of large-seeded tree species. In the Eastern Himalayas, large hornbills are important seed dispersers of large-seeded and relatively rare tree species belonging to the families Meliaceae, Myrsticaceae and Lauraceae (Datta, 2001). Since only large birds with large gape widths are in a position to transport large seeds, given the close correlations of body size with gape size (Wheelright, 1985), I expect large-seeded species that are solely reliant on hornbills to be dispersal limited. Furthermore, other large frugivores such as primates, civets or ungulates are unlikely to act as substitute dispersers since in general they show little dietary overlap with hornbills (Datta, 2001). In contrast, a much wider assemblage of small to medium sized birds including barbets, mynas, bulbuls and the fairy blue bird may compensate for the decline in dispersal services for small-seeded tree species due to their ability to handle small seeds and also because small-seeded species are hypothesized to represent a low investment strategy for attracting many, generalist frugivores rather than few, specialized ones (McKey, 1975). Large seeds that have higher nutritional value, however, typify high investment dispersal syndromes for attracting few, specialized frugivores and thus promote tight relationships with few bird species amongst a larger frugivore assemblage (Howe and Vande Kerckhoeve, 1981 and Howe 1993).

Elimination of hornbills may have profound consequences for tropical forests by altering tropical tree diversity in favor of small-seeded species. Similar patterns are also likely to result from the elimination of any important large frugivores, whether bird or mammal, suggesting that in the future tropical forests could perhaps be dominated by small-seeded tree species at the expense of large-seeded ones (Peres and Roosmalen, 2002). Seed dispersers are often critical to disperser-tree mutualisms (Cordeiro and Howe, 2003) and play important roles in the ecological restoration of disturbed and fragmented habitats. Hornbills are irreplaceable dispersers for trees in Africa (Whitney et al.1998) and Asia (Datta, 2001, Kinnaird et al. 1996), and have been identified as key organisms in rainforest regeneration and restoration since they fly for long distances through rainforests dispersing a great diversity of seeds along the way. Ecological restoration of forests in Asia including India, and Africa may then depend on preserving the seed dispersal capabilities of hornbills in conjunction with plantation of tree species that both provide critical food resources to hornbills and other frugivores as well as contribute to forest diversity.

The Eastern Himalayas provide an ideal system for the test of hunting on seed dispersal mutualisms and the resulting consequences for forest structure. It is recognized as one of the eight 'hottest hotspots' of biodiversity in the world (Myers et al. 2000) and among the 200 globally important ecoregions (Olson and Dinerstein 1998).The Indian part of this biodiversity hotspot harbors about 5800 plant species, of which roughly 2000 (36%) are endemic, hosts 50% of India's 1200 bird species (Singh, 1994), and holds the northernmost rainforests In India.

This study attempts to determine how loss of dispersers may impact the dispersal and regeneration particularly of large-seeded tree species Elimination of large frugivores such as hornbills may lead to dense aggregations of undispersed seeds lying below large-seeded parent trees due to reduced disperser visitation, and subsequently enhanced seedling mortality and low regeneration for species susceptible to density-dependent mortality. Moreover, we suspect that hornbill declines will be more severe for large-seeded species than small-seeded one, and we test this by determining whether hornbill visitation and seed removal rates differ for large- and small-seeded tree species.

3. STUDY AREA

The study was conducted in one protected area (the ‘control’ region) Pakke National Park and Tiger Reserve (862 sq. km 26°54′N~ 27°16′N, 92°36′~ 93°09′E) in East Kameng district, located within the priority North Bank Landscape of the Eastern Himalayas biodiversity hotspot (Fig.1). The disturbed (hunted) sites included the Reserve Forests close to the periphery of each park, namely Papum Reserve Forest (RF) and Doimara RF of Khellong Forest Division.

Towards the south and south-east the park adjoins reserved forests and the Nameri National Park (349 sq. km) of Assam. To the east lies the Pakke river and Papum Reserve forest; to the west it is bounded by the Kameng or Bhareli river, Doimara RF and Eagle Nest Wildlife Sanctuary, and to the north again by the Bhareli river and the Shergaon, Forest Division. The sanctuary is delineated by rivers in the east, west and north and is drained by a number of small rivers and perennial streams of the Bhareli and Pakke rivers which are tributaries of the Brahmaputra. The terrain of all the study sites is undulating and while the altitude ranges from 100m to about 2000m, the accessible altitude of the study site is only about 100-600m. Both Papum (1064 sq. km) and Doimara RF (216 sq. km) fall in Khellong Forest Division.

The vegetation of this region is classified as Assam Valley tropical semi-evergreen forest 2B/C1 (Champion and Seth, 1968). Forests of Pakke are multistoried and rich in epiphytic flora, woody lianas, and climbers. Limited studies of the vegetation have recorded 343 woody species of angiosperms in the lowland areas with a predominance of Euphorbiaceae and Lauraceae (Datta, 2001) Major emergent species include *Tetrameles nudilora, Ailanthus grandis,* and *Altingia excelsa* (Singh 1991). The forests along the lower plains and foothills are dominated by *Polyalthia simiarum*, *Pterospermum acerifolium*, *Sterculia alata*, *Stereospermum chelonioides*, and *Duabanga grandiflora* (Singh 1991, Datta 2001). Evergreen species include A. *excelsa*, *Mesua ferrea*, *Dysoxylum binectariferum*, *Beilschmedia* sp., and other middle-story trees in the Lauraceae and Myrtaceae..

4. METHODS AND RESULTS

I. Large avian census

Hypothesis 1. The abundance of large hornbills is impacted by hunting

While studies of seed dispersal, regeneration and recruitment are central to this study of rainforest regeneration and restoration, censuses determine the impact of hunting of large avian dispersers and its correlation with patterns of seed dispersal and recruitment. We therefore, walked a total of 111 km across three protected sites located within Pakke Wildlife Sanctuary and three hunted sites located within Papum RF and Doimara RF of Khellong Forest Division during the peak fruiting period of our focal tree species (Summer 2006). Hornbill and large pigeon abundances were determined on the transect walks. The only birds to disperse our large-seeded tree species are three species of hornbills (Bucerotidae), the Great Hornbill (*Buceros bicornis*), the Wreathed Hornbill(*Aceros undulatus*) and Oriental Pied Hornbills (*Anthracoceros albirostris)*, as well as two large fruit pigeons, the Mountain Imperial Pigeon (*Ducula badia*) and the Green Imperial Pigeon (*Ducula aenea*). Although the Green Imperial Pigeon does disperse the seeds of our focal trees, we did not observe it feeding on any of our tree species during focal watches conducted in this study. The Green Imperial Pigeon (*Ducula aenea*) was also only observed once during a transect walk. All other frugivorous birds with smaller gape-widths such as barbets, bulbuls, mynas, fairy bluebird, do not disperse the seeds of our focal large-seeded tree species, although some may peck at the fruits of some of the trees (e.g. those of *Polyalthia simiarum*), and are thus fruit-thieves.

Two transects, one spanning a riverine habitat and the other a forested stretch were walked in each of the six sites, three times each to record bird abundances. Counts were conducted between 5:30 to 9 am which is the period when hornbills are active in feeding and calling (Sethi per obs.). Transects were walked at a slow, uniform rate of 1km/hr while carefully scanning the canopy for bird activity. For each detection, the following observation were made- the number of birds, whether seen or heard, the sex (where possible) and perpendicular distance from transects. We recorded the encounter rate (abundance per km) on a per day basis.

Results

All three species of hornbills showed far lower abundances in hunted than non-hunted forests during the time our focal tree species were in fruit. Mean abundances of the Great (GH), the Wreathed (WH) and the Oriental Pied Hornbills (OPH) were 96.7%, 83.1% and 71.9% lower in hunted than in protected forests (Fig. 1, 2 and 3). Conversely, the Mountain Imperial Pigeon (MIP), which is not actively targeted by hunters in our forests showed an increasing trend in hunted sites (Fig. 4). Competitive release has been shown to occur on islands and tropical forest fragments (Renjifo, 1999, Terborgh et al. 2001). Slightly higher populations of these pigeons at our unprotected sites, although not significant (Mann-Whitney U test for non-parametric data, $U = 131$, $P > 0.5$) might signify a gradual transition towards competitive release from their ecologically similar competitors, the hornbills. The Green Imperial Pigeon, a putative seed disperser was sighted only once at a protected site during this study.

Fig 1. Great Hornbill

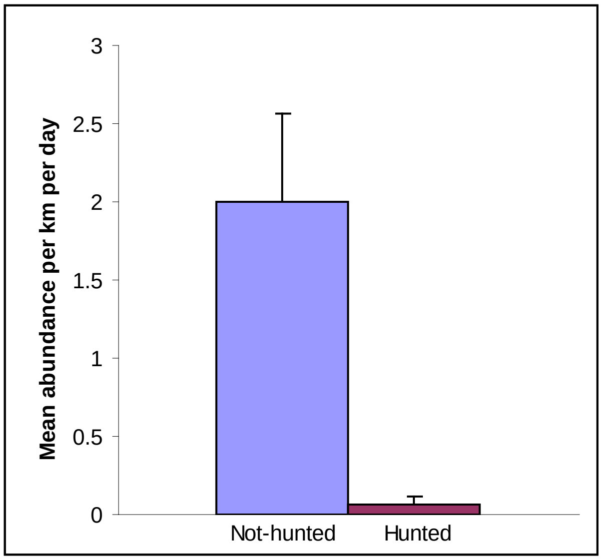


Fig 2. Wreathed Hornbill

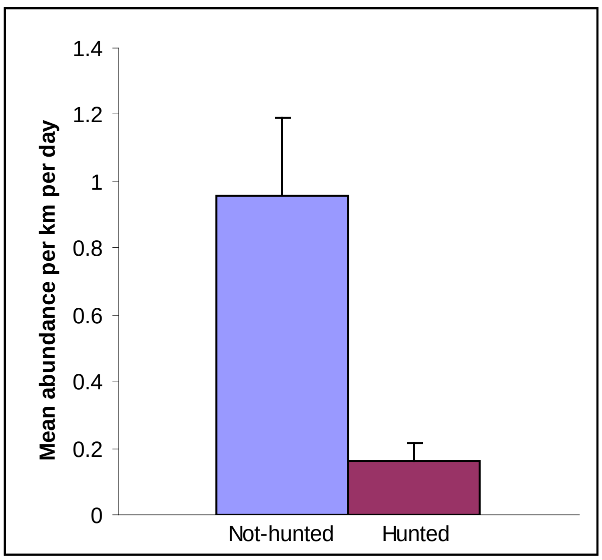


Fig 3. Oriental Pied Hornbill

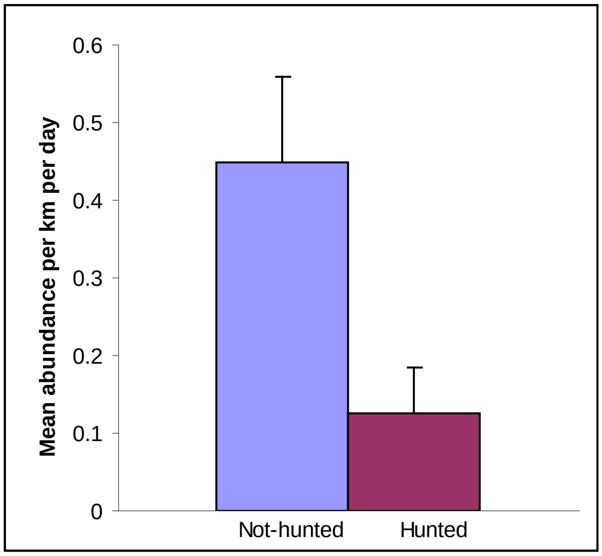
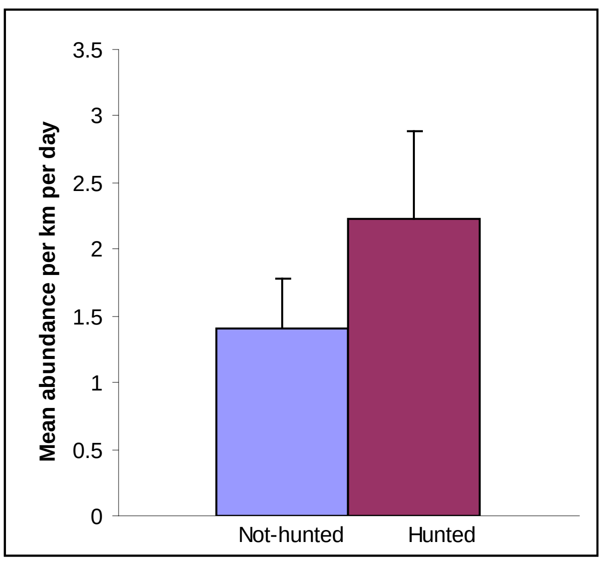


Fig. 4. Mountain Imperial Pigeon



II. Visitation rates and seed dispersal of large- and smaller-seeded species

Hypothesis 2. Hornbills are pivotal dispersers of large-seeded tree species but are not as important for smaller-seeded trees which rely instead on several species of small to medium-bodied birds

Only large birds with large gape-widths like hornbills can disperse large-seeded tree species while small and medium seeds can be dispersed by a bevy of other smaller birds such as bulbuls, mynas, barbets and the fairy blue bird. I therefore, hypothesize that large-seeded tree species in Pakke critically rely on hornbills for their dispersal but hornbills will make fewer visits and remove fewer seeds of smaller-seeded tree species than smaller-bodied birds.

I studied three large-seeded, arillate, capsular tree species; *Dysoxylum binectariferum*, *Chisocheton paniculatus* and *Amoora wallichii* (*Aglaia spectabilis)* belonging to the Meliaceae as well as *Polyalthia simiarum*, a drupe-bearing, large-seeded species (Anonaceae) which unlike the meliaceae species is highly fecund, often fruiting twice a year. The meliaceae species in contrast bear small fruit crops with long fruiting seasons and only a few fruit are dehisced at any one point. They, therefore, appear to depend on one to few dispersers that will reliably disperse their fruits, that is, they are specialized trees at the specialized end of the specialized-generalized continuum (sensu Howe 1993). *Polyalthia* on the other hand has more potential dispersers including civets and primates (pers. obs.) as well as bats (Kashmira Kakati, pers. comm.). *Polyalthia* while definitely more specialized than a small-seeded species appears to be less specialized than the capsular, arillate fruits of our meliaceae trees. Tree species with smaller, drupaceous seeds that attract many dispersers, apart from hornbills and *Ducula* pigeons include *Litsea monopetala* and *Cinnamomum bejolghota* (*C. obtusifolium*) (both Lauraceae).

To determine which frugivores eat the fruits of the focal species and the efficiency of seed dispersal, focal watches were conducted. One 12 hour watch was conducted at each focal tree. We conducted focal watches at 3, 9, 7, 9, 4 and 2 trees respectively (~408 hours of observation) of *Dysoxylum binectariferum, Chisocheton paniculatus, Amoora wallichii, Polyalthia simiarum, Litsea monopetala* and *Cinnamomum bejolghota* from March to August. Vertebrate visitors were identified and classified as dispersers (swallowed seeds and removed them from trees), predators (ate or destroyed seeds) or non-dispersers (dropped all seeds under parent crowns, or visited the trees but did not feed on fruit or seeds or just pecked at the fruit while leaving the fruit on the tree, i.e. fruit thieves). Visitation rates combined with seeds removed or dropped near parent trees provide an estimate of removal effectiveness for each frugivore species (Schupp, 1993). Seeds that are predated, dropped below trees or moved to arboreal caches have been classified as 'wasted', since they rarely contribute to the next generation of recruits.

Results

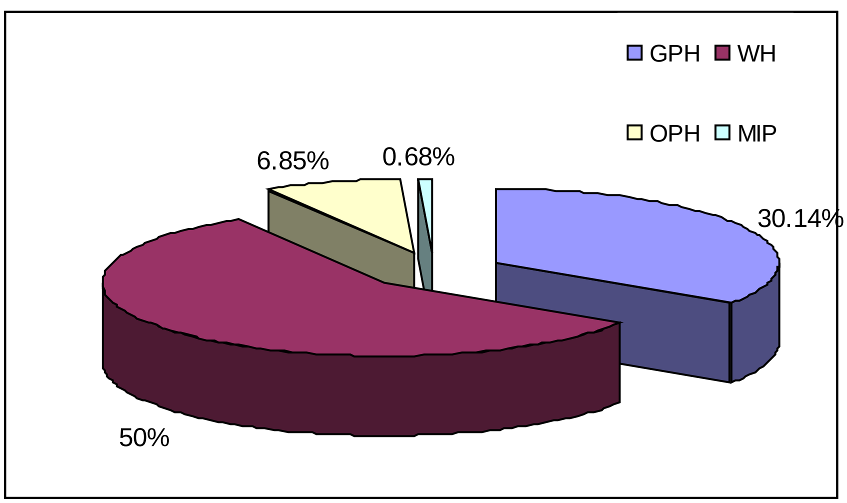
Our results indicate that visitation rates of large-seeded, arillate species (*Amoora wallichii*, *C. paniculatus* and *D. binectariferum*) are low, even in non-hunted sites with intact disperser assemblages. There is no evidence of removal by species other than hornbills and *Ducula* pigeons, indicating their critical role in the regeneration of these species. The large-seeded, widely distributed species, *Polyalthia simiarum* (Anonaceae), in contrast is dispersed by very many species. Three species of squirrels, act largely as seed predators, chewing and dropping seeds below parental crowns or moving them away to arboreal caches, where only in rare instances the few that may fall to the ground are likely to sprout. We have classified these seeds as being wasted.

A. Dispersal of large-seeded tree species

1. *Amoora wallichii*

Hornbills were the most important dispersers of *Amoora wallichii*, dispersing 87% of the seeds taken. Amongst the three hornbill species, the Wreathed Hornbill was the most important, dispersing 50% of the seeds taken. The Mountain Imperial Pigeon, however, dispersed a mere 0.67 % of all seeds taken (Fig. 5). Approximately, 87.67% of the total seeds taken were dispersed. The remaining 12.33% of seeds taken were dropped (wasted) by the Great Hornbill (0.68%), the Wreathed Hornbill (10.96%) or the Giant squirrel (0.68%).

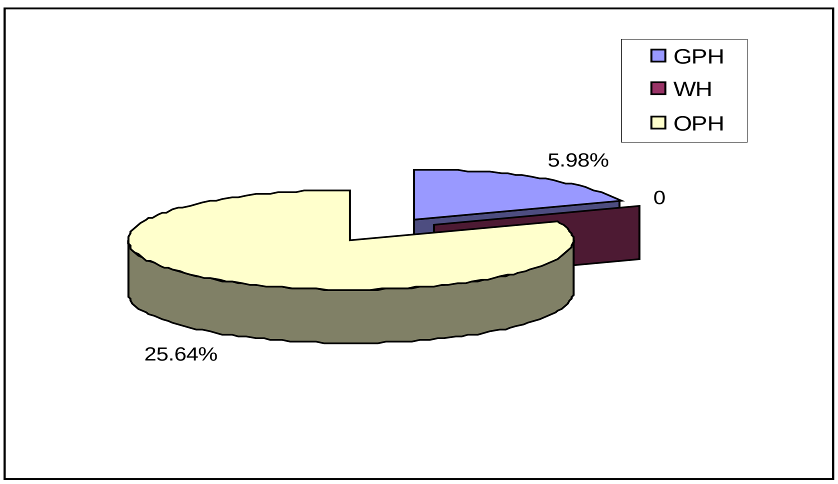
Fig. 5. Percentage of *Amoora* seeds taken that were dispersed (87.67%)



2. Chisocheton paniculatus

Hornbills were the only visitors to *Chisocheton* trees (25 visits) and removed 32 percent of all seeds taken (Fig. 6). Overall only 32% of the seeds were dispersed, the remaining seeds taken were all wasted. The Oriental Pied Hornbill removed the most seeds (26%). Squirrels dropped 55 percent of all seeds taken, while the Oriental and the Wreathed hornbill dropped 11.11% and 2.56% respectively. Interestingly, at one focal tree, Pallas squirrels carried away seven intact, non-dehisced capsules (~ 28 seeds) into the canopy-these are probably stashed away in arboreal caches, where the majority do not germinate. The Mountain Imperial Pigeon did not visit *Chisocheton* trees-they do not appear to prefer its seeds. This is substantiated by data collected in 2008 from >30 trees across six disparate sites-only 3 seeds were removed by the pigeons.

Fig. 6. Percentage of *Chisocheton* seeds taken that were dispersed (31.62%)

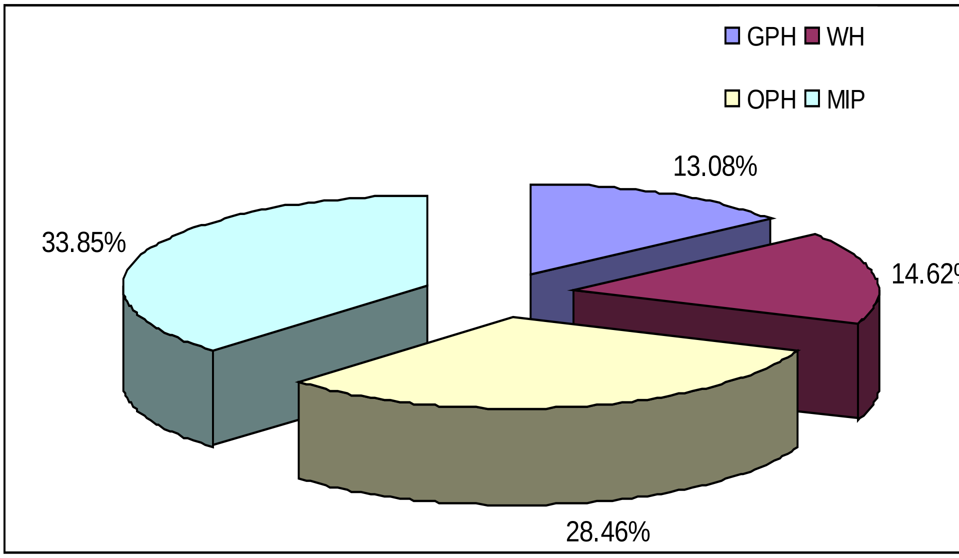


3. Dysoxylum binectariferum

Of all the large-seeded arillate trees, *Dysoxylum* had the most seeds dispersed and seemed to be a preferred forage species for both hornbills and the Imperial Pigeon. The Mountain Imperial Pigeon paid far more visits to *Dysoxylum* trees (30) than did the hornbills (17) and although it disseminated fewer (34%) seeds than the three species of hornbills combined (56%), it dispersed far more seeds than any of the individual hornbill species

(Fig. 7). Only 10 percent of all the seeds were dropped, 5.4 percent by hornbills, 3.8 percent by the Mountain Imperial Pigeon and 0.77 percent by the Hoary-bellied squirrel.

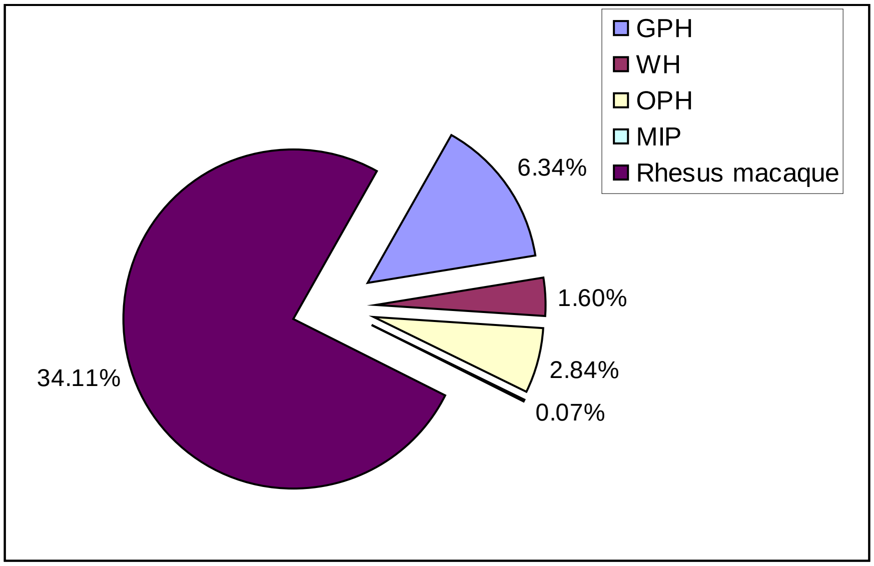
Fig.7. Percentage of *Dysoxylum* seeds taken that were dispersed (90.01%)



4. Polyalthia simiarum

Hornbills visited *Polyalthia* trees more frequently (19) than the rhesus (14) or the Mountain Imperial Pigeon (1). Hornbills dispersed 11 percent of all the seeds taken and the Imperial Pigeon 0.07 percent (Fig. 8). The rhesus macaque dispersed 34 % of the seeds, but it also dropped the most. The rhesus macaque only removed seeds from one tree located at the periphery of the forest-the rhesus is rarely seen in the forest interior. About equal proportions of seeds were dropped (55%) as were removed (45%). The rhesus dropped the most seeds (40%) followed by squirrels (10%) and then by birds (5%), including the hill myna (0.3%).

Fig. 8. Percentage of *Polyalthia* seeds taken that were dispersed (44.96%)

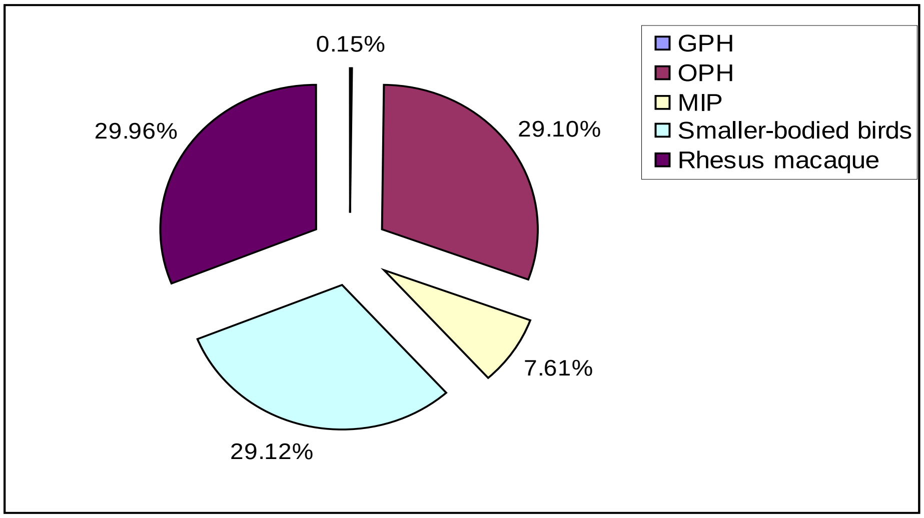


B. Dispersal of smaller-seeded tree species

1. *Litsea monopetala*

About equal proportions of the seeds of *Litsea monopetala* were dispersed by hornbills (29.2%), the rhesus macaque, and small birds (29.1 percent), while the Imperial Pigeon dispersed 8 percent (Fig. 9). Seeds removed by the rhesus macaque, however, were all from one tree located near the forest edge. Since rhesus macaques are not found in the forest interior, their actual contribution to dispersal of this tree in the protected area is likely to be low. When the data was reanalyzed without using the *Litsea* tree located at the park border that rhesus macaques visited, hornbills removed most (52.3%) of the seeds, small-bodied dispersers 33 percent and the Imperial pigeon 11 percent. Contrary to what was predicted, hornbills particularly the smallest of the three species, the Oriental Pied Hornbill, appear to be key dispersers for this species. Although, these trees are visited by numerous avian frugivores (a number of species of bulbuls, mynas and barbets), each of these small frugivores disperse only a few seeds at a time. In contrast, hornbills ingest large numbers of seeds per visit and removed significantly (P <0.005, Games Howell post-hoc tests) more seeds per visit (66.79 ± 18.96 seeds, N =14) than small-bodied birds (4.34 ± 0.43 seeds, N =164). Hoary-bellied squirrels carried away four seeds of this species to surrounding arboreal stashes/nests.

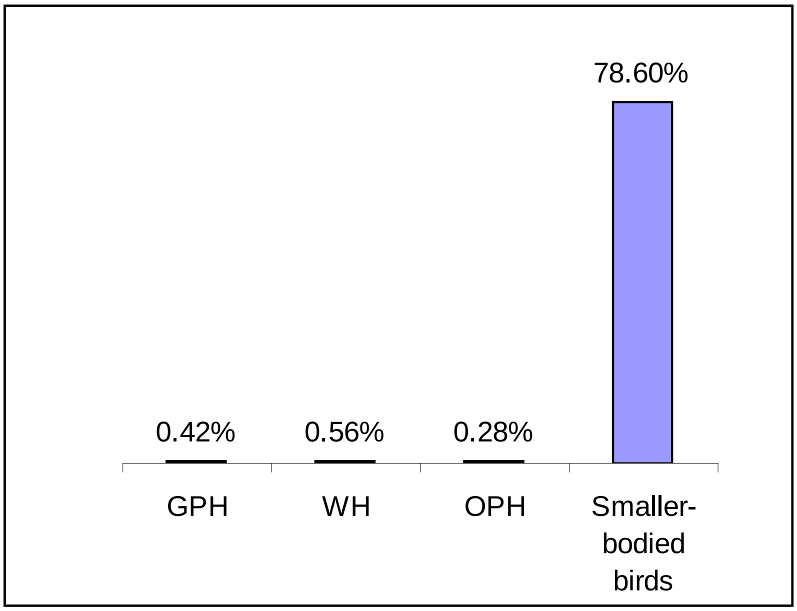
Fig. 9. Percentage of *Litsea* seeds taken that were dispersed (95.94%)



2. *Cinnamomum bejolghota*

Visitation and seed removal rates of *Cinnamomum bejolghota* suggests that this species fits the bill of generalized trees in the specialized-generalized continuum (Howe, 1993), that is, those trees that attract a generalized suite of dispersers and are not dependent on a restricted disperser assemblage. Hornbills removed only a fraction (1.3%) of seeds and small-bodied birds the overwhelming majority (78.6%), while the trees were not visited by the Mountain Imperial Pigeon. Hill mynas (*Gracula religiosa*) removed the most seeds (25%) followed by the Lineated barbet (*Megalaima lineata*) (15%) and the Blue-throated barbet (*Megalaima asiatica*). Far fewer visits (Welch $F_{1,20.406}$ = 11.866, P <0.005) were paid to each tree by hornbills (mean ± SE, 0.833 ± 0.401, N =6) than by small-bodied birds (9.364 ± 2.125, N =22). Of the seeds taken, 79.86% were dispersed and the remaining dropped. Birds dropped most of the seeds (15%) followed by squirrels (5%).

Fig. 10. Percentage of *Cinnamomum* seeds taken that were dispersed (79.86%)



III. Recruitment of tree species

Hypothesis 3. Elimination of large hornbills lead to reduced recruitment of large-seeded tree species in hunted versus non hunted sites. Recruitment of smaller-seeded tree species will remain unaffected.

I expect that reduced seed dispersal of large-seeded trees due to decreases in their primary dispersal agents (hornbills) will lead to seeds congregating near the parent tree where they may suffer increased density dependent mortality (Howe, 1993, Harms et al. 2000) either due to enhanced predation (Janzen 1970, Connell, 1971) or due to intra-specific competition (for space, nutrients, etc.). Therefore, this will lead to poor recruitment of seedlings, juveniles and saplings in hunted sites as compared to non-hunted ones. Because smaller-seeded tree species are dispersed by an abundance of dispersers, I do not expect them to show low recruitment in hunted sites.

Recruitment of seedlings (<30 cm in height), juveniles (30cm-1m height) and saplings (1-5 m) were enumerated in 40 m long, wedge-shaped transects with a 20 degree angle in a random direction away from the base of each focal trees. Wedge shaped transects give a better estimate than linear transects since seeds dispersed increase (πr^2) rapidly with distance (Howe, 1990). Wedges were laid out beneath 40 trees each of *Chisocheton*, *Dysoxylum* and *Polyalthia*. Ten trees of each species were selected from each site; two sites were protected and two were hunted. In the case of *Amoora*, a total of 15 trees were sampled, five each at two protected sites and five at one hunted site. *Amoora* is also an important timber species and our second hunted site did not have any adult representatives of this species. Trees had probably been felled sometime in the past. We also sampled six trees of *Actinodaphne obovata* in the protected sites and five trees at a hunted site. *Actinodaphne* has small to medium sized seeds. Although we had planned to sample more tree species with small seeds, we were unable to obtain a sufficient number of replicates across sites for a meaningful comparison.

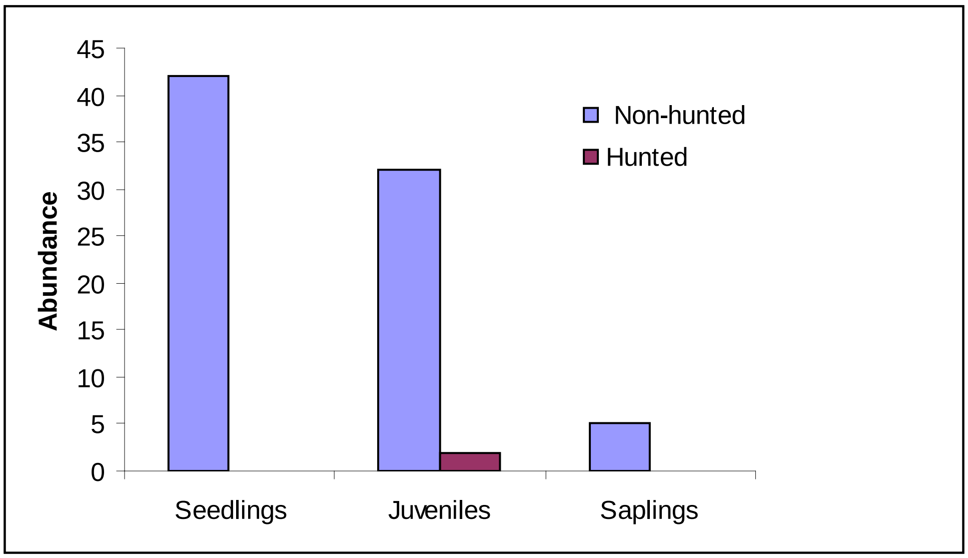
Within each wedge shaped transect, each seedling, juvenile and sapling was marked, and the height and basal diameter measured. Distance from the focal tree was recorded in 2 m segments, and distance to an additional conspecific and the forest edge were measured with a range finder. Data was analyzed using SPSS and all dependent variables (seedlings, juveniles, saplings) were log-transformed to meet assumptions of a normal distribution. One-way ANOVAS were carried out for groups with equal variances. Groups with unequal variances were analyzed using a Welch ANOVA.

A. Large-seeded tree species

1. *Amoora wallichii*

Overall recruitment of seedlings, saplings and juveniles of *Amoora* was 100% lower in disturbed than in protected sites. Hunted sites had no seedlings or saplings of this tree while 87.5% fewer juveniles recruited (Welch $F_{1,27.203}$= 8.212, $p < 0.009$) in hunted than protected sites.

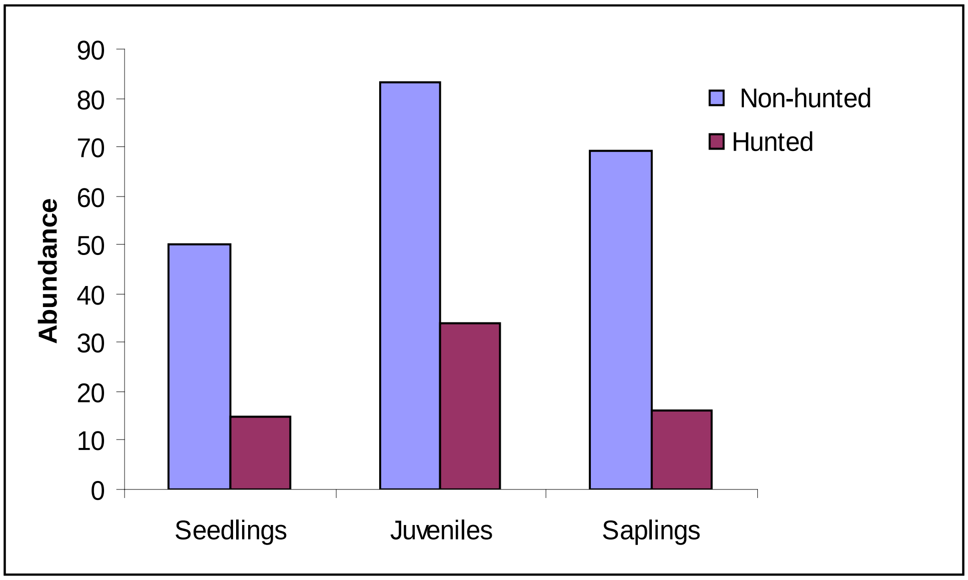
Fig. 11. Stage-wise abundance of *Amoora* in hunted versus non-hunted sites (N=15)



2. Chisocheton paniculatus

Overall recruitment of seedlings, saplings and juveniles of *Chisocheton* was 67.8% lower in disturbed than in protected sites. Numbers of seedlings, juveniles and saplings of *Chisocheton* were far lower in hunted than non-hunted sites (Fig. 12). Mean seedling abundance was 69.6% lower (Welch $F_{1,64.217}$ = 5.804, $p < 0.02$) in hunted than protected sites while mean juvenile abundance was also 59.13% lower ($F_{1,78}$ = 11.80, $p < 0.005$) in hunted than in protected forests. Mean sapling abundance was also 76.88% lower (Welch $F_{1,65.154}$= 17.971, $p < 0.0001$) in hunted than protected sites.

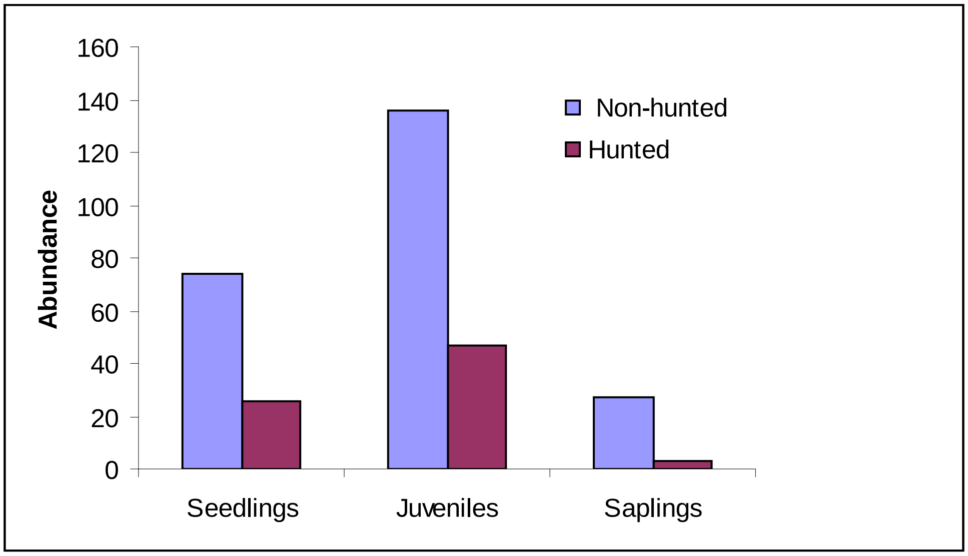
Fig . 12. Stage-wise abundance of *Chisocheton* in hunted versus non-hunted sites



3. Dysoxylum binectariferum

Recruitment of seedlings, saplings and juveniles of *Dysoxylum* was 67.9% lower in disturbed than in protected sites. Numbers of seedlings, juveniles and saplings of *Dysoxylum* were far lower in hunted than non-hunted sites (Fig. 12). Mean seedling abundance was 64.86% lower (Welch $F_{1,71.62} = 11.802$, $p < 0.002$) while mean juvenile abundance was also 65.29% lower ($F_{1,78} = 22.80$, $p < 0.0001$) in hunted than in protected forests. Similarly, sapling abundance was 88.24% lower (Welch $F_{1,47.388} = 6.890$, $p < 0.02$) in hunted than protected sites.

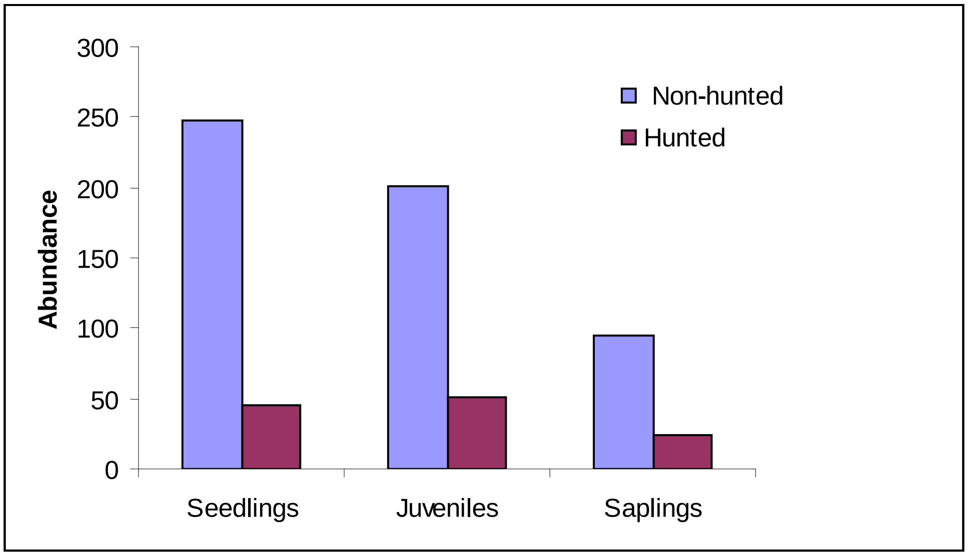
Fig. 13. Stage-wise abundance of *Dysoxylum* in hunted versus non-hunted sites



4. *Polyalthia simiarum*

Polyalthia recruitment was 77.9% lower in disturbed than in protected sites. Numbers of seedlings, juveniles and saplings of *Polyalthia* were far lower in hunted than non-hunted sites (Fig. 12). Mean seedling abundance was 81.72% lower ($F_{1,78} = 35.86$, $p < 0.0001$) in hunted than protected sites while mean juvenile abundance was also 74.55% lower (Welch $F_{1,72.396} = 23.909$, $p < 0.0001$) in hunted than in protected forests. Similarly, sapling abundance was 74.79% lower (Welch $F_{1,61.068}= 9.169$, $p < 0.005$) in hunted than protected sites.

Fig. 14. Stage-wise abundance of *Polyalthia* in hunted versus non-hunted sites

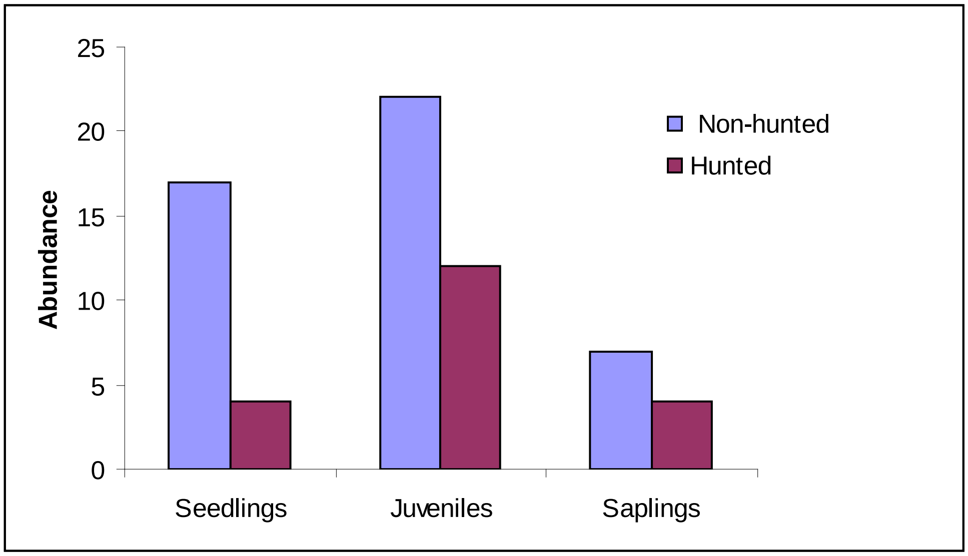


A. Smaller-seeded tree species

Actinodaphne obovata

As would be expected for a tree species with small-sized seeds that can be dispersed by umpteen small, medium and large-bodied avian dispersers, recruitment of *Actinodaphne obovata* was not significantly lower in hunted as compared with protected forests. Mean abundances of seedlings ($F_{1,20} = 3.039$, $p > 0.05$), juveniles ($F_{1,20} = 0.079$, $p > 0.05$) as well as saplings ($F_{1,20} = 0.298$, $p > 0.05$) were not significantly different across sites.

Fig. 15. Stage-wise abundance of *Actinodaphne obovata* in hunted versus non-hunted sites



Mean abundances were not significantly different across sites

5. DISCUSSION

Over-hunting is estimated to be second only to habitat destruction and degradation as a global cause of both current and predicted future species extinctions (Diamond and Case, 1986, Reid, 1992) and also plays a role in the disruption of ecosystem services such as dispersal. While hunting appears to leave the structure of forests unaltered, this is probably misleading since loss of fruit eating and seed dispersing animals may severely hinder the regeneration of fruiting tree communities through impeded seed dispersal.
In the Eastern Himalayas, altered patterns of seed dispersal due to hornbill hunting may change spatial patterns of seed and seedling regeneration, tree composition and forest diversity.

This study indicates that loss of hornbills may have severe repercussions for the regeneration and recruitment of forest tree species, especially large-seeded ones that are reliant on restricted disperser assemblages. Other factors such as logging, shifting cultivation and general forest erosion are likely to act in conjunction with hunting not only to decimate hornbill populations, but also to disrupt the essential services they perform to maintain forest composition and diversity. Our study, the first one in South Asia to describe the consequences of disturbance for plant-disperser interactions, indicates that this is indeed true for important hornbill-forage species.

Hornbill populations were much lower at hunted sites during the period my tree species were in fruit. This also corresponds to the period of peak fruit abundance in the forest (Datta, 2001) when local abundance should be highest. Moreover, while hunting in these forests has occurred for centuries, recent widespread felling in foothill reserve forests adjacent to protected areas coupled with extensive clearing of forests for jhum cultivation, may spell local extinction for some hornbill-disseminated trees.

The results clearly indicate that recruitment of large-seeded trees is severely impeded in hunted forests with severely depressed regeneration of seedlings, juveniles and saplings. As predicted, most large-seeded tree species are critically reliant on hornbills and in some cases Imperial Pigeons for seed dispersal and ultimately successful reproduction. This is especially true of capsular species such as *Amoora*, *Chisocheton* and *Dysoxylum*, where only hornbills and pigeons appear to be able to successfully remove seeds from dehiscent capsules. The relatively large-seeded, single-seeded drupe bearing tree *Polyalthia simiarum* in contrast produces abundant fruits that although large in size are relatively easy to handle by a larger disperser assemblage that also includes primates, civets and possibly bats. Nonetheless, this species is also recruitment-limited in hunted forests. Poor dispersal acting in conjunction with other factors resulting from the hunting and logging process such as altered populations and/or foraging strategies of seed predators, changes in abiotic regimes, etc. may all conspire to reduce recruitment.

Results are equivocal for smaller-seeded tree species. While they have much larger disperser assemblages, e.g. *L. monopetala* and *C. bejolghota*, evidently hornbills are very important for some of them, e.g. *L. monopetala* but not so for others. *Actinodaphne obovata*, for example did not demonstrate reduced recruitment at a hunted site as compared with a protected one. Additional studies of forest trees with small to medium sized seeds are required to assess their reliance on declining hornbill populations.

Studies on hunting practices in Arunachal clearly demonstrate its deep-rooted cultural and ritualistic nature (Aiyadurai, 2007) and community-driven conservation activities may be the only way to reduce hunting pressures. Doing so is imperative, given the numerous interlinked natural processes that are altered by bushmeat hunting. This study clearly underlines the adverse consequences of hunting of particular species for ecosystem services such as seed dispersal and highlights the crucial need for more such studies to document the effects of hunting for other pivotal animal-driven processes such as herbivory and seed and seedling predation. Protecting these biodiverse forests not only from hunting but from the other concomitant activities particularly illegal logging must become an urgent priority.

6. PUBLICATIONS AND FURTHER RESEARCH

Publications resulting from this research (The Rufford Foundation has been acknowledged in all manuscripts):

Completed

1. A paper on poor recruitment of large-seeded tree species at our study sites is in revision in Conservation Biology. We have received very positive reviewer comments and a revised version has just been resubmitted.
2. A paper on differential visitation and seed removal rates of large and small-seeded tree species is ready for submission to Biotropica.

In preparation

1. A paper on the recruitment of *Amoora wallichii*
2. Survival of large-seeded tree species

Additional studies: We are carrying forward the existing research in 2008 with additional funding to see if patterns observed in 2005-2006 remain consistent over multiple years.

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8. ACKNOWLEDGEMENTS

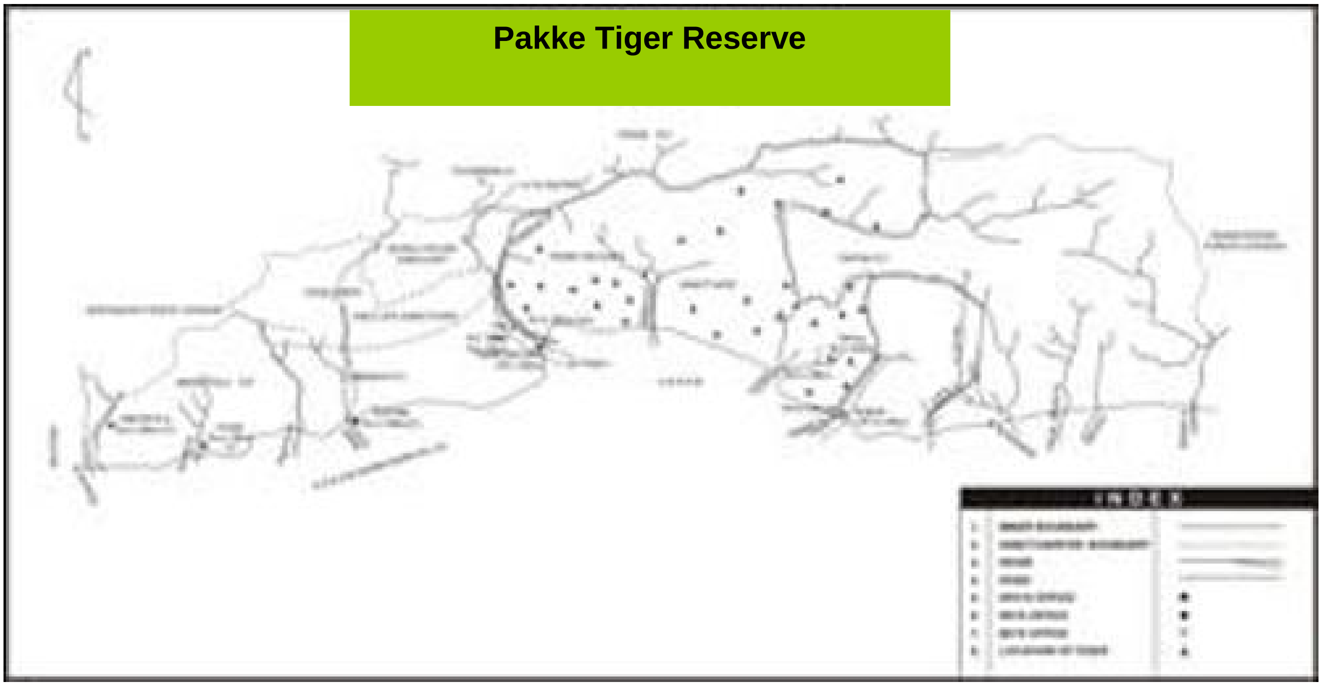
This study would not have been possible without the help of various people who gave unstintingly of their time and support. I wish to thank the Arunachal Pradesh Forest Department especially the Principal Chief Conservator of Forests for providing permission and numerous renewals so that I could finish the research. At Itanagar, C. Loma and P. Ringu helped me in innumerable ways. In the field, Tana Tapi made my stay comfortable. His enthusiasm, encouragement and company were invaluable as well as his support after my accident. All the officers, staff and mahouts of the Forest Department made my work in Pakke both possible and memorable. I am especially grateful to B. Isleri, R. Riram and C. Rana for their support and friendship. My fieldwork would not have been possible without all the help I received in the field from D. Tachung, G. Nath, B. Tejaram, M. Natung, S. Bagung, Motai, K.Wage and Ganesh.

My advisor, H.F. Howe continued to guide and support my work, despite the numerous delays and change of plans. N. Cordeiro gave me invaluable advice and encouragement. A. Datta first introduced me to Pakke and supplied information on sites and species that made this study successful. Hilaluddin provided help with bird censuses. I am very grateful to the Rufford Foundation for supporting this research. Ongoing field work is supported by the Wildlife Conservation Society, a Provost's award and University Fellowship from the University of Illinois at Chicago.

I thank the people of Arunachal Pradesh for their delightful company and hospitality. I dedicate this report to Taya Tayum, an indomitable spirit who lost his life in a car accident, as well as to the staff of the forest department who face insurmountable odds to protect these fragile forests.

9. APPENDIX

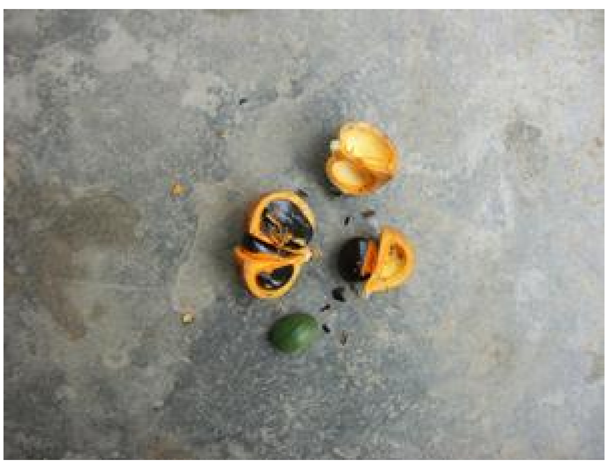
THE MAIN STUDY SITE (PAKKE TIGER RESERVE) AND SURROUNDING RESERVE FORESTS



10. PLATES

Polyalthia seeds in scat

Chisocheton capsule with last remaining seed



Dysoxylum capsule and seeds

Forests of Pakke