CHAPTER 8.

FRUITING PHENOLOGY AND PRE-DISPERSAL SEED PREDATION IN A RAINFOREST IN SOUTHERN WESTERN GHATS, INDIA

T. GANESH AND PRIYA DAVIDAR

Abstract
The mid-elevation non-dipterocarp wet forests in southern Western Ghats, India are some of the largest stretches of undisturbed forest remaining in this biodiversity hotspot. We established a long-term study of tree phenology in this forest to study the effects of biotic and abiotic factors on phenological patterns. We measured seed predation of selected canopy trees across three years. Seed predation intensity was measured through seed fall, phenology by fruit fall, and animal abundance through transect sampling. A total of 42 tree species was sampled for phenology and 35 species for seed predation intensity. Nine of these species fruited annually, seven fruited once in two years and the remaining species fruited once in several years. Two primates and two arboreal squirrels were the major seed predators in the forest. Primates were responsible for some intact seed dispersal, while squirrels were obligate seed predators. For numerous tree species seed predators were the only seed dispersers. Seed predator abundance showed no significant changes across years except for the case of the lion tailed macaque, which appeared to show seasonal population movement. No community-wide mass fruiting phenomena were noticeable in the forest but there was significant variation in fruit availability between years. A few tree species appeared to show mast fruiting in certain years. A majority of the species suffered high levels of seed predation. Seed predation intensity decreased during mast fruiting events for certain species while for others it had no effect. There was no difference in predation intensity between annually and supra-annually fruiting species. Masting as a means of overcoming high seed predation at the population level in the Western Ghats was limited to only a few tree species.

Key words: India, mast fruiting, phenology, seed dispersal, seed predation, tropical forest.

INTRODUCTION

Seed predation is an important ecological and evolutionary force affecting plant community diversity, demography, and phenology at individual, population and community levels (Harper, 1977; Hubbell, 1980; Schupp, 1988). Seed predation is

J. Lawrence Dew and Jean Philippe Boubli (eds.), Tropical Fruits and Frugivores: The Search for Strong Interactors 139 – 154.

affected by a multitude of factors ultimately related to fruit characteristics including plant spatio-temporal distribution, plant density, seed crop sizes, seed chemistry, seed size, season, ripening of fruits, soil humidity, temperature, pollination rates, predator density and the availability of alternative foods for generalist predators (see Crawley, 1992; Janzen, 1971). Fruit traits can have a major influence on predation levels since the primary functions of fruit morphology and chemistry are primarily seed protection and dispersal to safe sites.

Seed predation can also exert selective pressure to shape phenological characteristics and to favor traits such as mast fruiting that may reduce seed predation. It has been hypothesized that plants will synchronize fruiting to overwhelm seed predators (Janzen, 1974). This hypothesis has been supported by evidence from several tree species (Silvertown, 1980). However, it has not been demonstrated that masting evolved in response to predation since masting could also be a response to pollination by wind (Nilsson and Wastljung 1987; Smith et al., 1990). Masting phenomena have been consistently reported for temperate forests and the tropical rainforests of Southeast Asia but not for the Neotropics (Curran and Leighton 2000; Herrera et al., 1998; van Schaik et al., 1993).

Studies of phenology in Asia have focused primarily on dipterocarp forest trees which are wind-dispersed and which share similar fruit traits. Non-dipterocarp forests contain tree species with a variety of dispersal modes and phenological patterns (Newstrom et al., 1994). Consequently, we would expect that various forces shape their phenologies. There is at present no clear evidence of predator satiation by mast fruiting in non-dipterocarp forests. Thus, our primary research question was: does mast fruiting happen in non-dipterocarp Asian forests? Second, does mast fruiting always help reduce seed predation or are there some other benefits to the phenomenon?

In the Indian subcontinent many of the studies on phenology have come from dry tropical forests (Murali, 1992; Prasad and Hegde, 1986; Singh and Singh, 1992). The wet forests of Western Ghats have received very little attention (Kannan, 1994; Menon, 1993) and nothing is known about the mid-elevation forests of Southern Western Ghats which harbors a high proportion of endemic flora and fauna (Henry et al., 1982).

We started a long term regime of monitoring phenology, pollination, seed dispersal and floristic composition at a mid-elevation non-dipterocarp rainforest in the Western Ghats, India in 1990. The Western Ghats region is a global biodiversity hotspot. The Southern Western Ghats are the richest in terms of flora and fauna. These forests have been subjected to clearing for plantations and reservoirs, but nevertheless there are large stretches of rain forest left intact (Ramesh et al. 1997) and our site is the least disturbed site in the Western Ghats.

There is little information available on seed predation and frugivore abundance from forests in India. This paper therefore highlights information on seed predators and quantifies seed predation levels of selected tree species and relates it to fruit traits. Our specific aims were:

1. To quantify pre-dispersal seed predation of trees in a non-dipterocarp rainforest.
2. To determine whether seed predator abundance and fruit abundance are correlated.
3. To determine whether any salient fruit traits correlate with levels of seed predation.
4. To identify tree species exhibiting mast fruiting phenomena and to examine the effects of mast fruiting on predator satiation.

METHODS

Study area

The study was conducted in a wet evergreen forest at Kakachi in the Kalakad Mundanthurai Tiger Reserve. Kakachi ($8^o33'$ N. Lat.$77^o23'$ E. Long.) is located at 1300 m elevation and receives an annual rainfall of over 3500 mm, well distributed throughout the year. Mean maximum temperature is 24^o C and minimum 16^o C. The terrain is highly undulating and is drained by numerous mountain streams.

The vegetation at Kakachi is characterized by three dominant tree species, *Cullenia exarillata, Palaquium ellipticum* and *Aglaia bourdillonii.*(Ganesh et al., 1996). About 100 tree species have been recorded from the site (100 km^2) so far and over 100 species of birds and butterflies as well as 20 mammal species excluding bats. Several of these species are endemic to Western Ghats. Frugivorous birds are limited to only 6 species.

Phenology

Direct observation of phenology was done on a monthly basis by recording the percentage of the crown in flowers or fruits. Over 300 individuals from 70 spp. were followed from 1991 onwards. Fruit abundance was measured from linear fruit plots laid on the ground. Each plot measured 100 m x 0.70 m. Seventeen such plots covering a total area of 1170 m^2 were laid randomly in a 10 km^2 area. These plots were sampled once every two weeks from March 1991 to May 1994. All encountered fruit species were recorded, along with their abundances, and whether their fruits and seeds were eaten or aborted.

Animal observation

It was not always possible to closely observe fruit handling by seed predators as these animals were shy and difficult to see in the dense foliage and tall canopy. Fruit handling by seed predators was therefore observed opportunistically on all possible occasions. Dental marks left on partially eaten fruits were studied in order to obtain indirect data from frugivores that could not be directly observed.

Animal and seed abundance

A 3 km transect was monitored once every 15 days for animal presence and abundance. The transect was walked from 7 am to 10 am. All arboreal and terrestrial mammals were recorded. Fruits were collected from 53 species of canopy and subcanopy trees between 1991 and 1993 along forest trails with a total length of about 2.5 km. This constituted nearly 69% of the tree species in Kakachi (Ganesh, 1996) and 87% of the tree species that fruited during this period. The fruits were classified into 9 categories based on their size, weight, type, seed number, protection, and color. These classifications follow Gautier-Hion et.al. (1985).

Seed predation

For 35 tree species, predation levels were estimated by placing nylon nets of 1 m^2 under the crown. The nets sampled roughly 10% of the canopy area for each tree. The number of nets ranged from 1 to 10 with a median of 3. Nets were sampled once a week or once every 2 weeks depending on the phenology of the species. Species with prolonged fruiting episodes were sampled once every two weeks. Five trees per species were sampled except for the 5 most common species which had up to 10 trees sampled.

Fruits fallen in the nets were collected, sorted according to the damage to the seeds and animal species involved in the damage. The proportion of seeds damaged was calculated at the end of the fruiting period giving a percentage of overall seed predation.

RESULTS

Frugivore assemblage

The frugivore assemblage at Kakachi consists of five species of non-flying arboreal mammals, one flying squirrel, two species of bat, and six species of birds. Among mammals there are two tree squirrels, the Malabar giant squirrel (*Ratufa indica*) and the nocturnal giant flying squirrel (*Petaurista petaurista*), the Nilgiri langur (*Trachypithecus johnii*), the lion-tailed macaque (*Macaca silenus*), one species of civet, the brown palm civet (*Paradoxurus jerdoni*) and two species of frugivorous bats (*Cynopterus sp.* and *Rousettus leschenaultia*).

Apart from the civet and the two bat species, the other mammals are seed predators. In particular, the giant squirrel (*Ratufa indica*) the Nilgiri langur (*trachypithecus johnii*) and the flying squirrel (*Petaurista petaurista*) are the most important seed predators at the site. These animals may disperse seeds only accidentally either by spitting seeds after chewing the pulp as in the case of *Elaeocarpus munronii* by *S.johnii* or the accidental dropping of seeds while eating as in the case of *R.indica* feeding on *Cullenia exarillata* seeds. Avian seed predators belonging to the family Psittacidae (Parakeets) were not recorded at this site and none of the specialized avian frugivores were seed predators. Altogether, fruits of nearly 70% of the tree species at Kakachi are dispersed by these frugivores and seed predators.

Frugivore abundance

Giant squirrel (*Ratufa indica*): The density of *Ratufa indica* was found to be 46.71 ± 8.71 individuals per km^2 (n=41 censuses) and about 1 individual (mean=1.33) was encountered along the transect per census. Giant squirrels are territorial and mostly solitary.

Nilgiri langur (*Trachypithecus johnii*): While it was not possible to get a density estimate for these monkeys, the number of langurs sighted was 1.42 ± 0.44 per km (n=38 censuses).

Lion tailed macaque (*Macaca silenus*): A mean of 0.42 ± 0.19 *Macaca silenus* were recorded per km of transect (n=38 censuses). The 100ha site was usually occupied by a single troop of *M. silenus* comprising of 17 individuals. Smaller troops were encountered occasionally but it was not known whether they were part of the same troop or if they belonged to a different one.

Giant flying squirrel (*Petaurista petaurista*): It was not possible to estimate the density of *Petaurista petaurista*. Nevertheless, we estimated a mean number of 0.15 sightings per km (n=8).

Seasonal changes in frugivore abundance

Abundances of seed predators like *Ratufa indica* and *Trachypithecus johnii* did not differ between months (Wilcoxon signed test *R. indica*: T=0.41 df=9 $p<0.01$; *S.johnii*: T=-1.18 df=9 $p<0.05$; Fig. 1a, 1b). Lion tailed macaques were more commonly sighted during the dry season (February-May) and were sighted once during the wet season in June, 1991 (Fig. 1c). There was no significant difference in abundance of *Ratufa indica* between years (Kruskal Wallis test H=0.03 df=2, $p<0.05$) while it was significantly different for *S. johnii* (H=14.06 df=2, $p<0.01$). Fluctuations between months appeared to vary more in 1993 than in the previous years for all of the mammals.

Terrestrial seed predators like the Porcupine (*Hystrix indica*), small rodents (*Rattus sp.),* Mouse Deer (*Tragulus meminna*) and Wild Boar (*Sus scrofa*) were not sampled. Porcupine (*Hystrix indica*) and Mouse Deer (*Tragulus meminna*) were more commonly seen in the disturbed forest areas and were not common in the study site. There was little indirect evidence of the Porcupine (*H. indica*) in Kakachi.

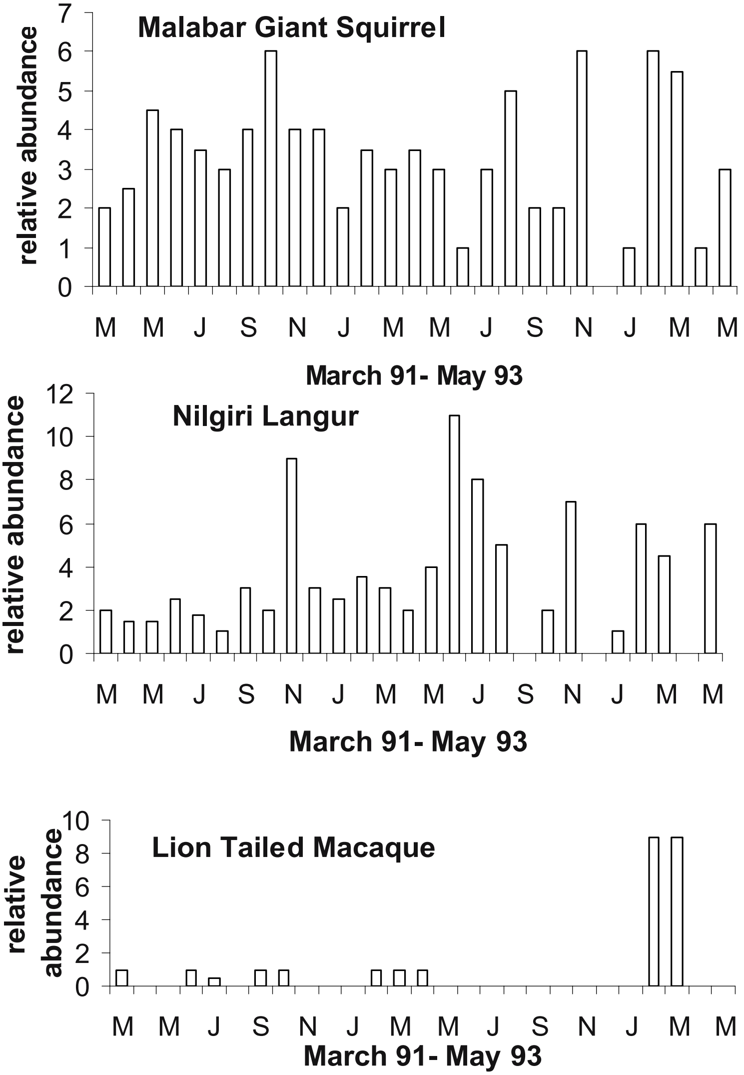

Figure 1. Abundances of seed predators as measured from transect censuses.

Community-level pre-dispersal seed predation

Seed predation levels varied from 1% (*Canarium strictum*) to almost 96% (*Aglaia sp*.) among the 35 tree species sampled. High seed predation (>70%) was found for two of the three species studied from the family Meliaceae. Members of the Elaeocarpaceae (2 spp.) and Rutaceae (2 spp.) had relatively low levels of seed predation (<30%). Members of the Lauraceae also had low levels of seed predation except for *Cryptocaria lawsoni* which was more frequently attacked by fruit galls. A large proportion (57%) of the tree species examined experienced higher than 50% seed predation during their fruiting period (Fig. 2).

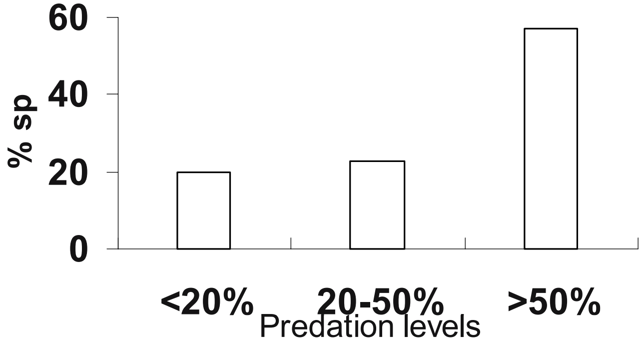

Figure 2. Frequency of seed predation across tree species.

Fruit characters and predation

Fruit characters can influence predators' choice of fruits and thereby the level of predation that a tree species suffers. Thirty two species whose seed predation levels were known were examined for fruit traits that might affect this variance in predation. Seed protection, as measured by seed coat hardness, showed a significant effect in lowering predation (Mann Whitney test U=180 N=32 $p<0.05$) while fruit protection did not have any significant effect in reducing predation (Mann Whitney test U=30 N=13 $p<0.01$). Species with protected seeds experienced a mean of 37% ± 8% damage (n=18) compared to 56 ± 5% (n=16) for species with unprotected seeds. Species like *Canarium strictum*, and *Acronychia pedunculata*, which had very hard seeds, suffered less predation while the presence of thick, hard, and thorny exocarps, as in the cases of *Cullenia exarillata, Myristica dactyloides,* and *Hydnocarpus alpina,* did not lower predation levels. In the case of *C. exarillata* there was a temporal change of predators across its fruiting period. The squirrel *Ratufa indica* preyed upon the fruit when it was unripe (all 36 observations) and preferred it less during the ripe stage (5/41 observations). The primates, *Macaca silenus* (30/41 observations) and to a lesser extent *Trachypithecus johnii* (6/41 observations) were the main predators of seeds in ripe fruit. There were no significant differences in predation between hard fruits and fleshy fruits (Mann Whitney test U=167 N=33 $p<0.05$). No significant relationship was found between seed number and predation.

Phenology

Fruit abundance in the forest as calculated from fruit traps was highly variable between years. Fruit abundance peaked in late 1993 and early 1994, and it was low during 1992 and early 1993. Fruiting species richness also increased in late 1993 and 1994 but showed less seasonal change within the year (Fig. 3). A Friedman two-way Anova corrected for tied ranks was performed to interpret the inter-year temporal variations in abundance. Results of these analyses show significant differences between years ($\chi^2 = 6$ df = 2, $p<0.05$). Pair-wise comparisons of years indicate that the differences between 1991 and 1992 ($\chi^2= 0.8$ df = 1,$p<0.05$) and 1992 and 1993 ($\chi^2= 1.8$, df = 1, $p<0.001$) were not significant but there was a significant relationship between 1991 and 1993 ($\chi^2= 7.2$ df = 1, $p<0.05$).

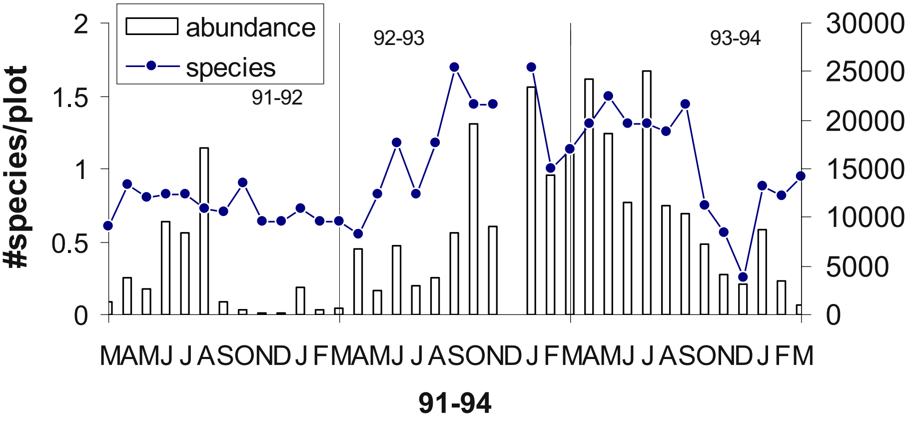

Figure 3. Fruit abundance and number of species in fruit from 1991 to 1994 in a wet evergreen forest.

Masting species

Among the 42 species of trees sampled in the plots, 9 species fruited annually while 7 species fruited twice and 19 species fruited only once. The remaining species were excluded from the above classification as the fruit plots sampled very few fruits of these species. Two species, *Tricalysia apiocarpa* and *Palaquium ellipticum*, showed clear masting patterns within the sampling period. *Tricalysia apiocarpa* mass fruited only once in 6 years with all individuals fruiting during the masting event (Fig. 4a). There was some fruiting by this species in the previous year but very few fruits were produced per tree. *Palaquium ellipticum*, on the other hand, fruited most years, producing fewer fruits per tree (Fig. 4b). In 1992 and 1993, several individuals were in fruit but none produced a large number of fruits. In 1991 and again in 1994 the species mast fruited and nearly all individuals were fruiting. This led to high overall fruit abundance in the forest. There were other species such as *Holigarna nigra* and *Callophyllum austroindicum* that fruited highly synchronously once in several years but these tree species were represented by few individuals in the sample.

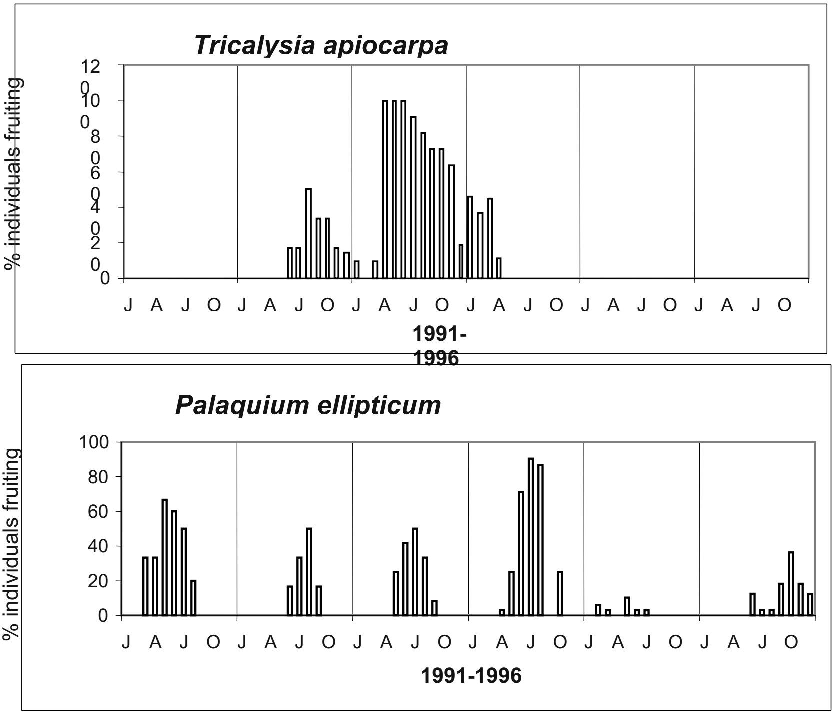

Figure 4. Fruiting phenologies of two non-dipterocarp tree species over six years.

Predation and length of fruiting season

There was a significant negative relationship between the length of the fruiting season (log) and the proportion of seeds eaten (arc sin transformed) ($r=0.50$ $n=26$ $p<0.05$). Species with short fruiting periods therefore experienced higher seed predation levels. Species for which the complete fruiting seasons were not available, such as *Callophyllum austroindicum,* were excluded from the analysis. Even within species there is a relationship between predation and length of the fruiting period. Length of the fruiting period differed between years for species like *Palaquium ellipticum*, which had fruits for a longer period in 1991 (3.6 months) than in 1992 (1.8 months) and which had correspondingly higher predation levels in 1992 (57%) compared to 1991 (11%). The proportion of individuals fruiting remained the same in both years.

Predation and frugivore abundance

There was no significant correlation between overall monthly mammal abundance and fruit abundance except for the case of *Ratufa indica*, where the relationship was negative ($r=-0.40$ $n=27$, $p<0.01$). This relationship with *R.indica* was probably more an artifact of sampling than a true decline. The abundance of lion tailed macaques in 1993 was possibly due to the higher availability of fleshy-fruits in the forest at that time.

Masting and seed predation

Annual comparison of seed predation levels was restricted to species for which a minimum of at least 100 fruits was collected from all the fruit plots pooled together within a year. Fruit plot data were used for this analysis because there were no differences between plot and net data for a particular season. (Mann-Whitney test $U=46$, $n=19$, $p<0.05$). Besides increasing the sample size, fruit plots also avoided bias in tree sampling. Mean fruit fall was calculated per plot and the corresponding proportion eaten was calculated.

If seed predation were the most important factor influencing masting, then we would expect highly preyed-upon species to show masting phenomena. Nearly 57% (20 spp.) of all the examined species suffer from high predation levels. Of these only 7 species, *Tricalysia apiocarpa, Palaquium ellipticum, Myristica dactyloides, Gomphandra coriaceae, Artocarpus heterophylla, Aglaia eleagnoidea,* and *Agrostistachys borneensis,* were abundant in the forest. Among these, *Gomphandra coriaceae, Myristica dactyloides, Artocarpus heterophylla,* and *P .ellipticum* fruit annually. The others mast once every several years. One species, *Aglaia eleagnoidea,* did not show masting behavior even though it did not fruit on an annual basis. There were two masting species for which we could collect data on seed predation across the phenological period, *T. apiocarpa and P. ellipticum*. The first of these, *T. apiocarpa,* suffered high levels of seed predation during mini masting and during its full masting period. Although there is a slight decrease in predation rates during periods of high fruit abundance, masting does not appear to produce any significant decrease in predation levels for this species.

Figures 6a and 6b illustrate the fact that seed predation levels fall as seed availability increases for only one of the two masting species. This phenomenon was seen for *P ellipticum* in 1991 when mast fruiting by this species corresponded with a drop in predation to a level below its three-year mean value (0.22).

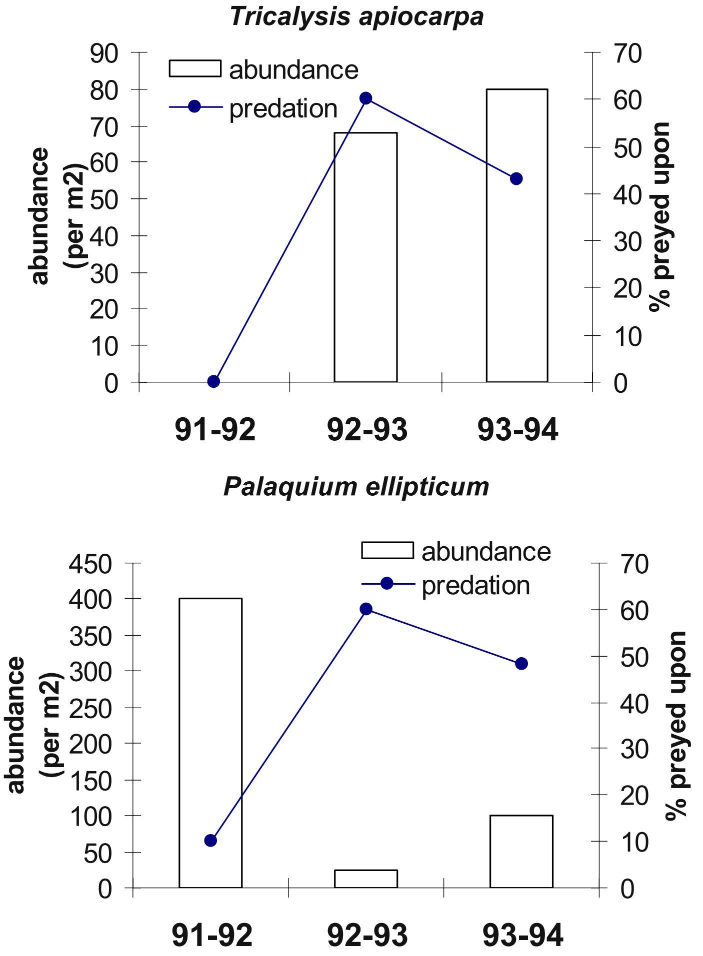

Figure 6. Fruit abundance and seed predation levels on two masting species across years.

DISCUSSION

Seed Predation

Pre-dispersal seed predation by arboreal mammals among canopy trees in Kakachi ranges from 1% to over 96%. These proportions vary between species and between years within species. Nearly all fruit species whether fleshy, hard, or protected, suffer from predation by vertebrates and 57% (20 out of 35) of the species suffer more than 50% pre-dispersal seed predation. These values are relatively higher than those reported for lowland Neotropical rainforests where post-dispersal seed predation is high (see Leigh and Alba, 1992; Terborgh et al. 1993). In Peru, seed predation is primarily restricted to post-dispersal predation (Terborgh 1990). In the M'Passa forest of Gabon, Gautier-Hion (1990) has shown a high diversity of arboreal seed predators, though levels of seed predation have not been quantified at the community level. In Southeast Asia, Leighton and Leighton (1983) note a high proportion of pre-dispersal seed predation by arboreal seed predators.

In Kakachi, pre-dispersal seed predation is higher than at sites in the Neotropics. This may be due to the high abundance of seed predators. Seeds form a major component in the diet of *Ratufa indica* (Borges 1993) and *Trachypithecus johnii* (Oates et al. 1980). The lion-tailed macaque, *Macaca silenus*, though a frugivore, also eats seeds (Menon, 1993). There is also some evidence that civets eat seeds of some species, because fragments of seeds were seen in their scats. Though seeds form only 25% of the diet of *T. johnii* (Oates et al., 1980) these squirrels consume many seeds because they are very abundant at this site. Based on his extensive survey of the Agasthyamalai hills, Oates (personal communication) found Kakachi to be the site with the highest known density of *T. johnii*. Similarly, *R. indica* seem to be at a higher density in Kakachi than in some forests (Ramachandran, 1988), but lower than in others (Borges, 1989).

A second reason for Kakachi's high levels of seed predation may be its proportion of fleshy-fruited trees, which occur at low densities compared to hard-fruited species (Ganesh, 1996). Seeds form nearly 57% of the edible biomass in fleshy fruits and are the only dietary resource for vertebrates in hard non-fleshy fruits (Ganesh, 1996). Seeds are also more nutritive and have a higher caloric value than pulp (Jordano, 1992). Even among Kakachi's dominant fleshy-fruited species like *P ellipticum,* seeds form the major resource for seed predators which tend to discard the pulp. Gautier-Hion et al. (1993) record higher proportions of seeds in the diets of African *Cercopithecus* monkeys in Zaire than in Gabon. They attribute this to a lower availability of fleshy fruits in Zaire than in Gabon, a phenomenon which is linked to impoverished soil. The Kalakad region of the Kakachi forest also has an impoverished red loamy soil (Ganesan and Parthasarthy, unpublished data) which may be a reason for the low number of fleshy-fruited species there. Another reason for the area's high level of seed predation could be the asynchronous fruiting pattern and low fruit production of many fleshy-fruited species like *T.apiocarpa Syzygium mundagam, Scolopia crenata*, and *Holigarna nigra.* In contrast, non-fleshy species like *Cullenia exarillata* and *Ormosia travancorica* fruit more regularly and their fruits are available for longer periods (Ganesh, 1995).

Fruit characteristics

In Kakachi and in Gabon, fleshy fruits had protected seeds, were either red, green, or orange and were commonly dispersed by birds (Gautier-Hion et al., 1985). At Kakachi, species with protected seeds had significantly lower predation levels than those with unprotected seeds. In contrast, in Gabon, species with protected seeds suffered high levels of pre-dispersal seed predation. Species which suffered high levels of seed predation in Gabon also had a greater diversity of seed predators and a different set of dispersers, whereas, for many species in Kakachi seed predators were the only dispersers.

Seed size may influence seed predation. Larger seeds have been described as more prone to predation (Janzen, 1969; Harper, 1977). In Kakachi the sizes of seeds ranged from a few mm to about 30mm in length (Ganesh, 1996). While all seeds studied suffered predation, *Trachypithecus johnii* ate seeds of all size classes while *Ratufa indica* ate only smaller seeds. Small hard seeds are avoided by *T. johnii* and *Macaca. silenus*. Two vertebrates, *M. silenus* and *R. indica* avoided eating the large seed of *Myristica dactyloides* and instead ate the aril while *T. johnii* consumed the seed. The reasons are not obvious, apart from the constraint of seed size, but seeds could have been avoided due to toxicity and/or nutrient availability (Janzen, 1969), which were not examined in this study.

Masting and phenology.

Synchronous seed production may have two important advantages. One is escape from predation pressure and the other is to take advantage of favorable climatic conditions for release and germination of seeds. There is an inherent difficulty in separating the two hypotheses, because mast fruiting could have evolved in response to either or both with the same effect. Terborgh (1990) suggested that for species that do not suffer from high seed predation, the release from predator pressure could lead them to show more random fruiting patterns. For such species masting events are of no importance with dispersal advantages overruling escape from predation. Some bird-dispersed species in Kakachi show this pattern. For instance, *Tricalysia.apiocarpa* does not have a significant reduction in predation when mast fruiting even though the predation levels are high (T.Ganesh, pers. obs.). These *T. apiocarpa* trees fruit for an extended period of several months but most of the predation happens in the unripe fruits. Birds disperse whatever seeds escape this onslaught later in the trees' fruiting period.

Previous authors have stated that the influences of seed predators on fruit traits might overwhelm those imposed by seed dispersing frugivores. The case in Kakachi may be different. It appears that a combination of disperser attraction and seed predation avoidance could have evolved together to benefit from mast fruiting. The case of *Pallaquium ellipticum* in Kakachi is pertinent here. The mast fruiting of this species attracts bats (*Cynopterus* spp.) and these bats were abundant in 1994 and to lesser extent in 1991 when this plant was mast fruiting. In other years when fruiting was low the seeds were found to be preyed upon by squirrels and monkeys. Predation levels on seeds in non-masting years were very high (Fig. 6b). This tree species did not evolve a thick protective seed coat but may have evolved a dual strategy to overcome seed predation and at the same time attract seed-dispersing fruit bats by mast fruiting. Yet another strategy would be to swamp predators early in the fruiting season so that enough fruits escape initial onslaught to remain and become ripe for seed dispersers later on in the season. One species, *Tricalysia apiocarpa,* may have has evolved such a strategy. Its fruits are not preyed upon when ripe and masting appears to have no effect on seed predation (Fig. 6a). However, the sheer amount of fruits produced by this species increases the chance that there are sufficient fruits that are ripe and available to dispersers several months after fruiting begins. Masting here is therefore useful at the initial tail of the fruiting period and dispersers are more important later on in the season.

In conclusion, fruits in the rainforests of Kakachi appear to be affected strongly by vertebrate seed predation during the pre-dispersal stage. Strong protective features of fruits and seeds appear to be a result of selection imposed by vertebrate seed predators. However, masting as a phenomenon is not only applicable for swamping seed predators but perhaps also for attracting seed dispersers. Therefore, seed predation should be considered in combination with seed dispersal in the study of these plant/frugivore interactions.

ACKNOWLEDGEMENTS

We are thankful to the Tamil Nadu forest Department for the necessary permission to do this work and the Tamil Nadu Electricity Board for giving us logistic support during the field study. We also thank the anonymous reviewers for critical comments. We are also grateful to Larry Dew and Jean Philippe who invited us to present this paper in their symposium in Panama.

REFERENCES

Borges, R. M. (1993). Figs, Malabar Giant Squirrels, and fruit shortages within two tropical Indian forests. *Biotropica, 256*, 183-190.

Crawley, M. J. (1992). Seed predators and plant population dynamics. In Fenner, M. (ed). *Seeds: Ecology of Regeneration.* London: CABI International, Great Britain, pp. 157-191.

Crome, F.H.J. (1975). The ecology of fruit pigeons in tropical northern Queensland. *Australian Wildlife Research, 2, 155*-185.

Curran, L., & Leighton, M. L. (2000). Vertebrate response to spatiotemporal variation in seed production of mast-fruiting dipterocarpaceae. *Ecological Monographs, 70,* 101-128.

Davis, S.D., V.H. Heywood, & A.C. Hamilton (1995). *Centers of Plant Diversity- A guide and strategy for conservation. vol 2. Asia, Australia and The Pacific.* Gland, Switzerland: WWF and IUCN.

Ganesan, R., & Parthasarthy, N. (manuscript). Seasonality of root production in the evergreen and semi evergreen forest of Kalakad-Mundanthurai Tiger reserve.

Ganesh, T. (1996). Fruting patterns among canopy trees and fruit use by vertebrates in a wet evergreen forest of the southern Western Ghats, India. Ph.D dissertation, Pondicherry University, India.

Ganesh, T., Ganesan,, R,. Devy, M.S., Davidar, P., & Bawa, K.S. (1996). An assessment of plant biodiversity at a mid-elevation evergreen forest of Kalakad Mundanthurai Tiger Reserve, Western Ghats, India. *Current Science 71,* 379-392.

Gautier-Hion, A. (1990). Interactiions among fruit and vertebrate fuit-eaters in an African tropical rain forest. In K.S. Bawa and M. Hadley (Eds.), Reproductive Ecology of Tropical forest plants. (pp 219-232), Paris: UNESCO and Parthenon Publishing.

Gautier-Hion, A., Gautier, J. P., & Maisels, F. (1993). Seed dispersal versus seed predation - an intersite comparison of two related African monkeys. *Vegetatio, 108,* 237-244.

Green, K. M., & Minkowski, K. (1977). The lion tailed macaque and its South Indian Rain Forest Habitat. In: G. H. Bourne, P. Rainier (Eds.), *Primate Conservation*. New York: Academic Press.

Harper, J. L. (1977). Population Biology of Plants, London: Academic Press.

Henri A. N., Chandrabose, M., Swaminathan M.S., & Nair. N.C. (1982). Agasthymalai and its environs: a potential area for biosphere reserve. *Bombay Natural History Society, 81*, 282-290.

Herrera, C. M., Jordano, P., Guitián, J. & Traveset, A. (1998). Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *American Naturalist, 152,* 576-594

Hubbell,S.P. (1998). The maintenance of diversity in a neotropical tree community: conceptual issues, current evidence, and challenges ahead. In Forest biodiversity research, monitoring and modeling: conceptual back ground and old world case studies. F. Dalmeier, & J. A. Comiskey (Eds.), MAB Series, Parthenon Publishing Group Ltd.

Jacobs, M. (1988). *The Tropical Rainforest.* Berlin: Springer-Verlag,

Janzen, D.H. (1969). Seed eaters versus seed size, number, toxicity and dispersal. *Evolution 23,* 1-27.

Janzen, D.H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics, 2*, 465-492.

Jordano, P. (1992). Fruits and Frugivory. In Fenner, M (Ed.) *Seeds: The ecology of regeneration in plant communities.* (pp. 105-156). London: CAB International.

Kannan, R. (1994). Ecology and Conservation of the Great Pied Hornbill (*Buceros bicornis*) in the Western Ghats of Southern India. Unpublished Ph.D. thesis, University of Arkansas, USA

Kinzey, W.G. & Norconk, M.A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Primatology. 81,* 5-15.

Kinzey, W.G & Norconk, M.A. (1993). Physical and chemical properties of fruits and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. International Journal of Primatology, 14, 207-227.

Leigh, E. G. Jr., & Alba G. de (1992). Barro Colorado Island, Panama: Basic Research and Conservation. *The George Wright Forum, 9,* 32-45.

Leighton, M. & Leighton, D.R. (1983). Vertebrate responses to fruiting seasonality within a Bornean rain forest. In Sutton, S.L., Whitmore, T.C & Chadwick, A.C, (Eds.), *Tropical Rain Forests: Ecology and Management* (pp. 181-209). Oxford, UK: Blackwell Scientific Publications.

Menon, S.A. (1993). Ecology and Conservation of the endangered lion-tailed Macacque, *Macaca silenus,* in the landscape mosaic of Western Ghats. Ph.D. thesis, Ohio State University, USA.

Murali, K.S (1992). Vegetative and reproductive phenology of a tropical dry deciduous forest, Southern India. Ph.D. thesis. Centre for Ecological Sciences, Indian Institute of Science, Bangalore.

Nilsson, S.G. & Wastljung, U. (1987). Seed predation and cross-pollination in moist seedling beech (*Fagus Sylvatica*) patches. *Ecology, 68,* 260-265.

Newstrom, L.E., Frankie, G.W., Baker, H.G. (1994). A new classification of plant phenology based on flowering patterns of lowland tropical rainforest trees at La Selva, Costa Rica. *Biotropica, 16,* 141-159.

Oates, J.F., Waterman, P.G., & Chos, G.M. (1980). Food selection by the South Indian leaf-Monkey, *Prebytis johnii*, in relation to food chemistry. *Oecologia, 45,* 45- 56.

Orians, G.H. (1969). The number of bird species in some tropical forests. *Ecology, 50,*783-801.

Peres, C.R. (1993). Shell strength and primate seed predation of nontoxic species in Eastern and Southern Africa. *International Journal of Primatology, 14,* 315- 343.

Prasad, S.N. & Hegde, M. (1986). Phenology and seasonality in the tropical deciduous forest of Bandipur, South India. *Proceedings of the Indian Academy of Sciences (Plant Science) 96,*121-133.

Ramachandran, K.K. (1988). Ecology and behaviour of Malabar Giant Squirrel *Ratufa indica maxima* (Schreber). *Kerala Forest Research Institute Report 55,* Peechi, Kerala.

Ramesh, B.R., Menon, S., & Bawa, K.S. (1997). A vegetation based approach to Biodiversity: Gap Analysis in the Agasthyamalai Region, Western Ghats, India. *Ambio, 26*, 529-536..

Schupp, E.W. (1988). Seed and early seedling predation in the forest understorey and in treefall gaps. *Oikos, 51,* 71-78.

Singh, J.S. & Singh, V.K. (1992). Phenology of seasonally dry tropical forest. *Current Science, 63,* 684-689.

Silverton, J.W. (1980). The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society, 14,* 235-250.

Smith, C.C., Hamrick, J.L. & C.L.Kramer. (1990). The advantage of mast year for wind pollination. *American Naturalist, 136,* 154-166.

Terborgh, J. (1986). Community aspects of frugivory in tropical forests. In: A Estrada & T.Fleming (Eds.), *Frugivores and Seed Dispersal* (pp 371-384). Dordrecht, the Netherlands: Junk Publishers.

Terborgh J. (1990). Seed and fruit dispersal - Commentary. In K.S. Bawa and M. Hadley (Eds.), *Reproductive Ecology of Tropical Forest Plants* (pp. 181-190). Paris: UNESCO and Parthenon Publishing.

Terborgh, J., Losos, E., Riley, P., & Riley, M.B. (1993). Predation by vertebrates and invertebrates on the seed of five tropical tree species of an Amazonian forest. *Vegetatio, 108,* 375-386.

Van Schaik, C. P., Terborgh, J., Wright, S.J. (1993). The phenology of the tropical forests, Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics, 24,* 353-377.

Ashoka Trust for Research in Ecology and the Environment (ATREE), 659, 5th A, Main, Hebbal, Bangalore 560024, India; Salim Ali School of Ecology and Environmental Sciences, Pondicherry University, Pondicherry 605014, India.