
Fruit Biomass and Relative Abundance of Frugivores in a Rain Forest of Southern Western Ghats, India
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Fruit biomass and relative abundance of frugivores in a rain forest of southern Western Ghats, India

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ABSTRACT. Fruit biomass and frugivore abundance were quantified over 3 y in a rain forest of the south Western Ghats, India. Fruit biomass was estimated by sampling fruit fall in the primary forest, and frugivore abundance by a 2.5-km transect. A total of 645 kg ha^{-1} of fruit was produced annually in the forest. Only 49% of this is edible to the frugivores and the remaining 51% is in the form of non-edible husks. Mammalian frugivores outnumbered avian frugivores and the majority of the mammals were seed predators. The total fruit biomass produced at Kakachi is lower than in the lowland forest and mountain forests in the neotropics but higher than in the wet sclerophyll forest of Australia. Lower diversity of trees and edaphic factors at Kakachi could be some of the reasons for these differences. On the other hand, paucity of fleshy fruits, low density of trees producing fleshy fruits and irregular fruiting of these species, account for the low number of obligate avian frugivores at Kakachi.

KEY WORDS: fruit biomass, frugivores, relative abundance, seed predators, Western Ghats, wet forests

INTRODUCTION

Tropical rain forests are by far the richest terrestrial ecosystems in the world. Much of this diversity is accounted for by the richness of frugivores, which are wholly or partly dependent on flowers, fruits and seeds (Howe 1986). However, the patterns of frugivore richness in tropical forests are not uniform both within and between continents. The lowland rain forests of the neotropics have the richest assemblage of frugivores while many sites in Malaysia and Africa are depauperate in them (Fleming *et al.* 1987, Willson 1991). These differences

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have been generally attributed to differences in abundance and diversity of fleshy fruits (Howe & Westley 1986) and to some extent on the diet preferences of individual species (Terborgh & van Schaik 1987).

Pan-tropical comparisons, however, have been severely hampered by the lack of concurrent availability of fruit biomass estimates and frugivore abundance from tropical sites. Moreover the impact of fruit seasonality on frugivore abundance is poorly understood especially how annual cycles of frugivores are tied to fruit biomass and how fruit availability varies across years (Levey *et al.* 1994). From the wet forests of the Western Ghats in India, which harbour a global hot spot of biodiversity, studies have often focused on a single frugivore species such as hornbills and lion-tailed macaques (Green & Minkowski 1977, Kannan 1994) and community-level analyses of frugivore richness are non-existent.

From the perspective of conservation of biodiversity it is important to understand biotic interactions in intact forests and how these interactions might be disrupted and what might be the consequences. Further, fruit biomass estimates and its variation across years can be useful in determining the overall productivity of the site and help in devising management plans for conserving frugivore populations (Snyder *et al.* 1987). The present study is an addition to this database and gives the first quantitative estimate of fruit biomass from an intact wet forest of the Western Ghats, India which supports one of the largest populations of the endangered lion-tailed macaque (*Macaca silenus*). The overall objective of this study was to estimate the quantity of fruit produced in the forest throughout 3 y and to assess the assemblage of avian and mammalian frugivores at the site and their relative abundance over the years. These are later compared with other sites to put Kakachi in perspective.

STUDY AREA

This study was conducted at Kakachi (8°50′ N latitude and 77°30′ E longitude) in the Kalakad–Mundanthurai Tiger Reserve at the southern tip of the Western Ghats of India (Figure 1). Kakachi was part of a contiguous forest of over 1000 km^2 and the study was carried out in the primary evergreen forest located on a northeast facing ridge of 300 ha with an elevation ranging from 1200 to 1550 m. The ridge was *c.* 1 km from the boundary of a tea plantation. The whole area is in the watershed zone for the Manimuthar river and receives over 3500 mm of rain annually which occurs twice in a year with a brief dry period between them. The mean maximum temperatures at the site ranged from 17 to 28 °C and the minimum temperature from 14 to 19 °C. The period from October to January is usually cold and misty. The mid-elevation evergreen forest at the site is a subtype of the more widespread *Cullenia–Palaquium–Mesua* series described by Pascal (1988) (Ganesh *et al.* 1996) and forms the primary habitat of the endangered lion-tailed macaque (*Macaca silenus*). About 173 plant species comprising 42 canopy trees, 48 understorey trees, 50 shrubs, 19 ground

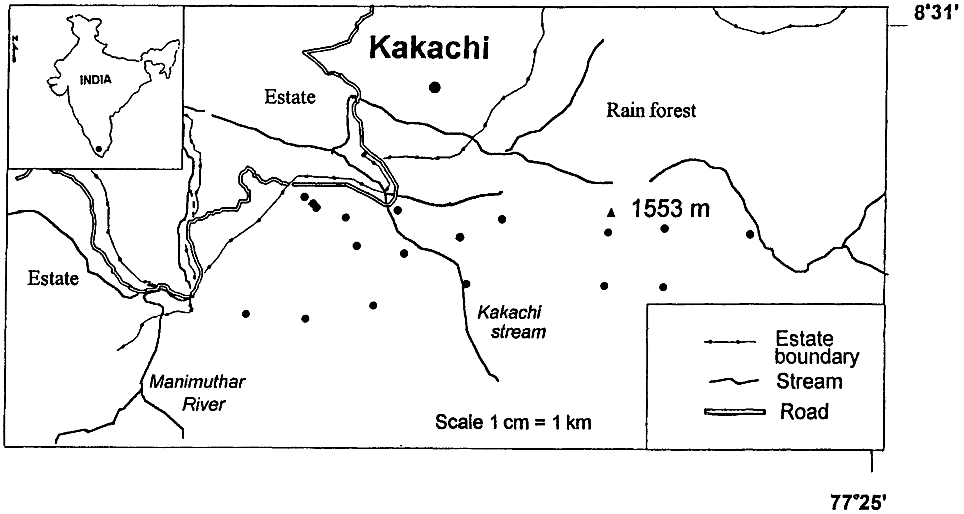

Figure 1. Map showing the study area within the Kalakad–Mundanthurai Tiger Reserve in the southern Western Ghats of India. Location of plots (•) used in estimating the fruit biomass are also shown. The map is only approximately to scale.

herbs and 15 woody lianas were recorded from 3.82 ha at Kakachi (Ganesh *et al.* 1996).

METHODS

Fruit biomass

Community-level estimates of fruit biomass in tropical forests have been obtained by sampling fallen fruits at periodic intervals over a specific area (Blake *et al.* 1990, Chapman *et al.* 1994, Foster 1982, Smythe 1970, Terborgh 1983). In Kakachi a similar method was used. Sixteen plots, each of 100-m × 0.70-m were laid on the forest floor in the undisturbed tall forests with few *Ochlandra* pockets (= bamboo brakes of lower elevation forests). They covered a mosaic of habitats with natural gaps and stream edges. These plots sampled a total area of 0.112 ha.

Sampling fallen fruits usually leads to an underestimate of true fruit production because of unaccounted fruit removal by the frugivores from the tree or even from the ground (Terborgh 1986). In Kakachi, to overcome this bias an attempt was made to quantify ground removal of fruits by vertebrates. Close to the fruit plots, sample plots were established, and baited with known amounts of fruit. The fruits were censused once a week. The species used for the baits varied with the season and all fruit species were subjected to this treatment whenever available. Results of these indicated that fruit removal for 95% of the species was not evident within the sampling interval of 15 d. For the remaining species there was some removal but only the seeds were eaten leaving behind a non-edible exocarp. It was therefore possible to quantify the number of fruits/seeds removed by the frugivores for such species and incorporate it into the total fruit fall.

Sampling was undertaken from March 1991 to March 1994. The number of plots initially was 11, subsequently increased to 16 in September 1992. Plots were marked permanently and sampled once every 15 d for the entire period of 3 y. Between November to December 1992 no sampling could be made as the area was inaccessible due to a cyclonic storm. During each sampling period, all the fruits (eaten or not eaten) fallen within the plots were collected, sorted to species and counted. Fruits were later put back into the forest away from the plots. A few unidentified fruits were preserved in 70% alcohol for later identification.

A minimum of 10 ripe fruits on trees or freshly fallen fruits, were collected and weighed using a digital balance. The mean of these were multiplied by the total fruits for each species recorded from the fruit plot to arrive at the biomass (wet weight) per species. Biomass was calculated separately for each plot and the cumulative total was obtained on a kg ha^{-1} basis.

Fruits were also categorised into bird, mammal and dehiscent fruits based on the size, type of fruit and on direct observations of fruit use by vertebrates. This was to facilitate analysis across frugivore taxa. Bird fruits were usually small (<15 mm) in diameter and were fleshy. Mammal fruits were large (>30 mm) and had a hard/fibrous exocarp. Dehiscent fruits had an inedible tough exocarp. Very few of these dehiscent fruits were arillate and dispersed by mammals or birds (Ganesh 1996).

Plant species were identified based on flower/fruit characters using Gamble (1928) and were later confirmed with herbarium specimens at the Botanical Survey of India, Coimbatore.

Relative abundance of frugivores

A transect of 2.5 km length was marked through the primary forest covering all available habitat types. The transect was walked at fortnightly intervals in the morning between 07h00 and 11h00 preferably under sunny weather conditions.

Mammals. Each transect was walked at a slow pace of 1 km h^{-1} noting the arboreal mammals seen in the vicinity of the path. For monkeys, number of troops encountered along the transect was recorded but it was not possible to estimate the exact number of animals in a troop every time. Each species was classified as seed disperser/predator based on direct observations and from Ganesh (1996).

Birds. For avian frugivores number of birds seen during the first 1.5-km length of transect was recorded. The entire length of the transect was not used as bird activity decreased after the initial 1.5 h of census. Sometimes, the bird census was not done along with mammal census because bad weather conditions were more detrimental for observations of birds than mammals. Birds were classified as frugivores based on Ali & Ripley (1987) and on personal observations. Some species, which eat fruits regularly such as the hill mynah (*Gracula religiosa*), were not included in this study as they were very rare. Additional sighting records of frugivore species not encountered in the transect, but along casual walks, were included to estimate the total frugivore richness of the area. Relative abundance was calculated as sightings per km.

RESULTS

Fleshy fruit availability

A total of 53 species of plants of which 42 were trees (canopy and understorey), six liana, four shrubs, and one epiphyte were sampled. This accounted for 47% (42/90) of the tree species available at the site. The other trees were either rare or did not fruit during the study period. Figs (*Ficus* spp.) were not common and did not figure in the sample. Fleshy fruits were produced by 70% (37 spp) of the total species sampled while the remaining produced dehiscent fruits of which only six species were animal dispersed, the rest were passively (not necessarily wind) dispersed. Twenty-six species (70%) of the fleshy fruits were dispersed by birds and the remaining 30% by arboreal mammals like civets, bats and primates.

Fruit biomass

During the 3 y, fruit biomass varied from 544 to 751 kg ha^{-1} with a mean of 645 ± 85 kg ha^{-1} y^{-1}. Corresponding seed biomass ranged from 130 to 207 kg ha^{-1} y^{-1} with a mean of 177 kg ha^{-1} y^{-1} (Table 1). The major contributors to the fruit biomass were *Myristica dactyloides* (Myristicaceae), *Palaquium ellipticum* (Sapotaceae), *Ormosia travancorica* (Papilionaceae) and *Cullenia exarillata* (Bombacaceae) which together accounted for 80% of the fruit biomass in the 3 y.

The actual consumable biomass available to frugivores and seed predators were seeds (27%) and pulp (22%), accounting for 49% of the total fruit biomass. The remaining 51% consisted of hard and inedible exocarps. Seeds are the major edible component of the fruit biomass constituting nearly 56% of the consumable biomass. However only arboreal mammals and no avian frugivores eat seeds (avian seed predators like parakeets and some pigeons were absent). Hence, only the fleshy pulp, which constitutes 4% of the edible fruit biomass, is available for the avian frugivores (Table 1).

Fruiting syndromes

Among the three categories of fruits, bird fruits were the most common with 23 species (43%) followed by mammals with 13 species (25%) and dehiscent with 12 species (23%). The remaining five species could not be categorised. In

Table 1. Total fruit, seed and pulp biomass at Kakachi, a rain forest site in the south Western Ghats across 3 y and for three syndromes. Percentages are in parenthesis.

	Biomass, kg ha^{-1}			
	1991	1992	1993	Mean
Fruit				
Bird	5	55	72	44
Mammal	268	93	203	188
Dehiscent	479	395	365	413
Total	751	543	640	645
Seed				
Bird	1	6	48	19
Mammal	95	21	52	56
Dehiscent	111	103	93	102
Total	207 (28)	130 (24)	193 (30)	177 (27)
Pulp				
Bird	4	49	24	26
Mammal	173	72	151	132
Dehiscent	368	292	272	311
Total	544 (72)	413 (76)	447 (70)	469 (73)
Edible pulp	171 (23)	92 (17)	159 (25)	141 (22)
Non-edible pulp	374 (50)	321 (59)	288 (45)	328 (51)
Total edible biomass[1]	378 (50)	222 (41)	352 (55)	317 (49)

[1] Total edible biomass = edible pulp biomass + seed biomass.

terms of biomass, however, dehiscent fruits contributed 64% to the total fruit biomass followed by mammal fruits (29%) and bird fruits (7%). Seed biomass also showed a similar pattern in the three categories (Table 1).

Fruit biomass, tree diversity and density

There was no significant correlation between tree density in the 16 plots and fruit biomass (Spearman's $r_s = 0.13$, $n = 16$, $P = 0.16$) and fruit abundance ($r_s = 0.41$, $n = 16$, $P > 0.01$). Tree species richness also did not correlate with number of species in fruit in each plot ($r_s = 0.30$, $n = 16$, $P > 0.01$). Log transformation of the data also did not improve the above correlations.

Frugivore assemblage

The arboreal frugivore assemblage at Kakachi consisted of four species of non-flying mammals, one flying squirrel and a bat, and six species of avian frugivores. Frugivorous arboreal mammals include two tree squirrels, the Malabar giant squirrel (*Ratufa indica*) and the nocturnal common giant flying squirrel (*Petaurista petaurista*), two primates, the Nilgiri langur (*Trachypithecus johnii*) and lion-tailed macaque (*Macaca silenus*), one civet, the brown palm civet (*Paradoxurus jerdoni*) and one species of frugivorous bat (*Cynopterus sphinx*). Avian frugivores included two species of pigeons – the imperial pigeon (*Ducula badia*), the Nilgiri wood pigeon (*Columba elphinstonii*), three species of bulbuls – black bulbul (*Hypsipetes madagascariensis*), yellow-browed bulbul (*H. indica*) and red

Table 2. Number of tree species at Kakachi dispersed and predated by frugivores during 1991–1993.

Family	Species	Number of plant species (%)		
		Dispersed	Predated	Total
Mammals				
Sciuridae	*Ratufa indica*	2 (5)	40 (95)	42
Cercopithecidae	*Trachypithecus johnii*	2 (7)	27 (93)	29
Cercopithecidae	*Macaca silenus*	5 (63)	3 (37)	8
Birds				
Columbidae	*Ducula badia*	15 (56)	0	27
Pycnonotidae	*Hypsipetes madagascariensis*	17 (63)	0	27
Pycnonotidae	*H. indica*	14 (52)	0	27
Megalaimidae	*Megalaima viridis*	17 (63)	0	27
Others[1]		13 (42)	0	31

[1] Includes civets and bats.

whiskered bulbul (*Pycnonotus jocosus*), and one species of barbet – the small green barbet (*Megalaima viridis*).

All of the four species of arboreal mammals were seed predators (two squirrels and two primates). Of these, the giant squirrel and the Nilgiri langur alone ate seeds of over 90% of the tree species (Table 2). Birds were exclusively dispersers and no evidence of seed predation was noticed. Known seed crushing pigeons were absent.

Relative abundance of frugivores

The Nilgiri langur and the giant squirrel were the most commonly sighted mammal frugivores (Table 3). There was no significant difference in encounter rates between them (Kruskal–Wallis test, $H = 2.76$, $P > 0.05$). On the other hand, the lion-tailed macaque was seen less often in the area and usually one or two troops were sighted with the largest troop comprising 17 individuals. The sighting rates differed between the squirrel and the macaque ($H = 43.32$, $P < 0.001$) and the langurs ($H = 46.51$, $P < 0.001$). Among avian frugivores, yellow-browed bulbul and black bulbul were the most common species and had

Table 3. Mean (± SE) sighting rates (km^{-1}) in the rain forest of Kakachi in south Western Ghats, India. The mean is pooled from all transects in a year. Number of transects run for mammals were 18 in 1991, 21 in 1992 and 12 in 1993. For birds it was 16 in 1991, 19 in 1992 and 12 in 1993.

Species	1991	1992	1993	Pooled
Mammals				
Ratufa indica	1.62 ± 0.57	1.25 ± 0.65	1.40 ± 0.87	1.42 ± 0.70
Trachypithecus johnii	0.94 ± 0.77	1.27 ± 1.17	1.40 ± 1.39	1.20 ± 1.11
Macaca silenus	0.12 ± 0.23	0.07 ± 0.16	1.08 ± 1.89	0.42 ± 0.76
Birds				
Ducula badia	0.27 ± 0.40	0.40 ± 0.45	0.67 ± 0.33	0.45 ± 0.40
Columba elphinstonii	—	0.03	—	0.03
Hypsipetes madagascariensis	1.22 ± 1.09	0.87 ± 0.89	1.41 ± 1.27	1.16 ± 1.08
H.indica	0.89 ± 0.43	1.27 ± 0.77	1.93 ± 0.61	1.36 ± 0.61
Megalaima viridis	0.11 ± 0.38	0.17 ± 0.29	0.29 ± 0.35	0.19 ± 0.34

similar sighting rates. Imperial pigeons and barbets were rarer than the bulbuls ($H = 42.63$, $P < 0.01$) while the Nilgiri pigeon was the rarest and was seen only in 1992 (Table 3). Red whiskered bulbul was found only along forest edges and hence not encountered in the transect.

Between-year variation

Fruit and seed biomass. The total fruit, seed and pulp biomass show the same trend among years (Table 1). However, differences exist among the three syndromes. Fruits of species dispersed by birds differed significantly between years ($\chi^2 = 18.20$, df = 2, $P < 0.001$). This was mainly due to differences between 1992 and 1993. In 1993 both fruit and seed biomass was higher than in the other years (Table 1) but was not significantly different between 1991 and 1992, and between 1991 and 1993. Pulp biomass of bird fruits decreased in 1993 from the previous year whereas seed biomass continued to increase because of more seedy species fruiting like *Beilschmedia wightii* and *Mastixia arborea* in 1993. The low bird fruit biomass in 1991 was not due to sampling bias as differences in the number of plots between years was weighted and expressed as kg ha^{-1}. Comparison was also made with the same number of plots between years, the results were similar to those obtained above. No significant difference between years was observed for fruits and seeds dispersed by mammals ($\chi^2 = 4.35$, df = 2, $P > 0.05$) and those which were dehiscent ($\chi^2 = 0.67$, df = 2, $P > 0.05$). However, even though there were no significant differences between pairs of years for mammal-dispersed and dehiscent fruits, mammal-dispersed fruits and seeds were less than half in 1992 compared with 1991 and 1993 (Table 1).

Frugivores. Based on all transects run in a year, there were no differences in relative abundance of lion-tailed macaque ($H = 1.10$, $P = 0.58$), Nilgiri langur ($H = 0.42$, $P = 0.80$) and giant squirrel ($H = 2.64$, $P = 0.26$) between years. However, in 1993, encounter rates of lion-tailed macaque were high compared with other years (Table 3).

Among avian frugivores only relative abundance of yellow-browed bulbul was different between years ($H = 12.46$, $P < 0.01$). These were significantly higher in 1993 compared to 1991 ($H = 10.91$, $P < 0.01$) and 1992 ($H = 7.04$, $P < 0.01$). The other avian frugivores did not statistically differ between years but were generally higher in 1993 (Table 3).

DISCUSSION

Fleshy fruits are associated with dispersal by vertebrates. In Kakachi nearly 70% of the sampled species produced fleshy fruit which were eaten by vertebrate seed dispersers. Similarly in other tropical forests 70–90% of the plant species are vertebrate dispersed (Alexandre 1978, Howe 1986, Jordano 1992, Willson 1991) with a maximum number found in the lowland rain forests of the neotropics (Howe 1986, Jordano 1992) and lower values from Africa and south-east Asian forests (Howe 1986, Jordano 1992, Dowsett-Lemaire 1988, Willson 1991). In the tropical forests of Australia fleshy fruits are more abundant in the understorey than in the canopy (French 1991, Willson *et al.* 1989) while at many sites in south-east Asia vertebrate dispersed plants are few because of diversity of wind dispersed dipterocarp species (Willson 1991). While dipterocarps are absent in Kakachi, wind dispersal is restricted only to a few liana species. Therefore, it appears that the proportion of fleshy fruited species among canopy trees in Kakachi forest are lower than those from lowland forests of neotropics but appear to be similar to some African sites (Howe 1986).

Seventy-five per cent of tree species in Kakachi experienced pre-dispersal seed predation by arboreal mammals. Very few studies have examined pre-dispersal seed predation by vertebrates at a community level. A recent study at Kakachi by Ganesh (1996) has reported that seed predation intensity by arboreal mammals varied from 1 to over 80% per species with the greater proportion of them experiencing over 50% seed loss. High levels of seed predation have been reported by parrots in the forests of Brazil (Galetti & Rodrigues 1992), arboreal mammals in Lopé and Gabon in Africa (Gautier-Hion *et al.* 1986) while lowland tropical forests from Peru experience low levels of pre-dispersal seed predation by arboreal mammals (Janson & Emmons 1990). High levels of seed predation may be linked to higher numbers of seed predator species. For instance, in Kakachi and Gabon the common diurnal arboreal frugivores are seed predators (Ganesh 1996, Gautier-Hion *et al.* 1986) while in Peru such obligate dependence on seeds by arboreal mammals is minimal (Janson & Emmons 1990).

Fruit production

The wet forest at Kakachi produced about 645 kg (wet weight) ha^{-1} y^{-1} of fruits per year which ranged between 544 to 751 in the 3 y. Although liana, shrubs and epiphytes were under-represented in the sample, their contribution to the biomass may not be high as they are few in number and small in size. Despite incorporating large eaten fruits into the fruit sample at Kakachi, the fruit biomass was almost three times lower than the values obtained from lowland forests of Peru and Panama (Table 4). It is also lower than the mountainous Luquillo experimental forest of Puerto Rico but exceeds those from the moist altitudinal forest of south-eastern Brazil, Zimbabwe and the wet sclerophyll forest of Australia. Although data are available on fruit biomass from other sites in Africa and south-east Asia they are not strictly comparable as these values are given in dry weight of fruit and are lower than the wet weight biomass at Kakachi (see Leigh & Windsor 1982, Pascal 1988). It is likely that most of the south-east Asian forests produce less fruits than others (Terborgh & van Schaik 1987) though little is still known on a regional scale of the differences between these forests.

Table 4. Fresh (wet weight) fruit biomass, tree species number and density from different sites.

Site	Fruit biomass ($kg\ ha^{-1}\ y^{-1}$)	Number of tree species	Density (ha^{-1})	Forest type	Source
Cocha Cashu Peru	1990	201	673	Lowland rain forest	Terborgh (1993), Gentry (1990)
Panama	2180	93	512	Lowland forest	Smythe (1970), Gentry (1990), Foster (1982)
Puerto Rico[1]	600	61	776	Rain forest	Lugo & Frangi (1993), Wadsworth (1951)
Brazil[1]	160–400	NA	NA	Montane semi-deciduous forest	Morellato (1992)
Zimbabwe	7–559	NA	NA	Riverine	Durham (1990)
Australia	7–37	12	655	Wet sclerophyll	French (1991)
India	645	53	812	Wet evergreen forest	Present study R. Ganesan; unpubl. data

[1] Dry weight, the rest are all wet weight.
NA, not available data.

Causes of low fruit biomass

On a local scale, within the contiguous 300-ha forest sampled, fruit biomass was not significantly related to vegetation density or plant species richness but on a larger continental scale it may be one of the reasons for the lower fruit biomass value at Kakachi. Lugo (1992) mentions that the species composition of a forest stand could lead to differences in fruit fall. In Puerto Rico, areas with low species diversity corresponded with lower fruit biomass (see Lugo & Frangi 1993). At Kakachi 53 tree species (> 10 cm dbh) were encountered in 1 ha (R. Ganesan; unpubl. data) which is lower than Panama, Peru and Puerto Rico, whereas stand densities are comparable (Table 4) (see Gentry 1990).

Edaphic factors may also influence fruit biomass. Forests growing on poor soils are generally less productive than those in fertile alluvium soils (Terborgh & van Schaik 1987). Wet forest areas in Kalakad–Mundanthurai Tiger reserve have red loamy soils which are not very fertile (R. Ganesan; unpubl. data) and could possibly account for lower fruit biomass compared with the forests on richer soils in the neotropics.

Frugivore diversity: the dominance of mammal seed predators

The majority of the arboreal mammals in Kakachi are seed predators (Ganesh 1996). Gautier-Hion *et al.* (1993) suggest lack of fleshy fruit availability as a reason for the high levels of seed predation. They demonstrate this hypothesis from the change in diet of the *Ceropithecus* monkeys in East Africa in relation to fleshy fruit and seed availability. In sites of low fleshy fruit availability monkeys preferred to be seed predators. At Kakachi 56% of the edible biomass is due to seeds and the majority of the dominant plant species produced only seeds as a resource. Not only is overall seed biomass high at Kakachi, it is mainly produced by dehiscent fruits which show less variation between years than fleshy fruit types. Therefore a reliance on seeds is more favourable compared to fleshy fruits (typically bird fruits) which are more unpredictable.

Avian frugivore diversity and fruiting species: why are there so few species?

In the Western Ghats nearly 22 species of birds can be considered to be relatively more frugivorous than other fruit eating species (Ali & Ripley 1987). Only 27% of them are found in Kakachi. No comparable data are available on frugivore richness at a similar elevational range of Kakachi elsewhere in the Western Ghats, but at lower elevations of 900 to 1000 m which harbour the moist deciduous forests, it is higher in Anamalai (Kannan 1994) and Kalakad (T. Ganesh; unpubl. data).

Despite low avian frugivore diversity at Kakachi, nearly 50% of the plant species are bird dispersed. This is comparable to the number of bird-dispersed species in many other wet forests of the neotropics, west Africa and south-east Asia (Gautier-Hion *et al.* 1985, Janson 1983, Leighton & Leighton 1983) but is intriguing when one notices the low number of avian dispersers. Such low diversity of dispersers has been reported from the high altitude temperate rain forest of Chile (Willson 1991). Although nearly 65% of the species in Chile are vertebrate dispersed, very few species of birds account for their dispersal (see Willson 1991). Willson (1991) suggested, this may be due to higher abundance of frugivores and lack of seasonality shown by them, assuming the density of fruiting species are comparable with other sites. In Kakachi, on the contrary, there is a seasonal flux of some avian frugivores like the black bulbul and imperial pigeon. They occur in high abundances and remove disproportionately large numbers of fruits (Ganesh 1996). Besides, the density of bird-dispersed species is also low compared with other vertebrate-dispersed species and many of these such as *Tricalysia apiocarpa*, fruit supra-annually making fruits an unreliable resource (Ganesh 1996). Over an annual time scale very few bird-fruit species fruited and the sudden outburst of supra-annual species did not increase the diversity of the bird species in the area (Ganesh 1996).

Another reason could be the paucity and rarity of figs (*Ficus* spp). There are three species of *Ficus* in Kakachi and all of them are rare (Ganesh *et al.* 1996; R. Ganesan, *pers. comm.*). Figs are an important resource for birds elsewhere in the Western Ghats where up to 23.6% of the avifauna feed on their fruits (Kannan 1994). This has also been reported from Peru (Terborgh 1983), Malaysia (Lambert & Marshall 1991) and Borneo (Leighton & Leighton 1983). Hornbills (*Buceros bicornis*) which rely heavily on figs (Kannan 1994) are also missing at Kakachi, but occur at lower elevations in the Kalakad hills where fig diversity and density are probably higher (T. Ganesh; *pers. obs.*).

This study sampled canopy and common understorey trees such as *Gomphandra coriacea* which although have a high density and did fruit regularly every year, lost most of the unripe crop to seed predators (Ganesh 1996). This resulted in very few fruits ripening and available for avian frugivores like yellow-browed bulbul which forage mostly in the understorey and subcanopy (T.Ganesh; *pers. obs.*). Many tropical and temperate forests support a higher abundance of fleshy fruits among shrubs (Levey *et al.* 1993, Willson 1991) and a corresponding higher number of frugivorous bird species. In Kakachi, Krishnan (1994) showed low abundance of fruits produced by shrubs and nearly 40% of them were non-zoochorous dehiscent fruits. The remaining species, even though bird-dispersed, fruit asynchronously with small fruit crops (Krishnan 1994). This may be the reason for the lower diversity of avian frugivores in the understorey as well, because there is no record of any hunting or other major disturbance in the patch both in the past and present. The frugivore–fruit interactions described here can therefore be considered intact.

Frugivore abundance

Kakachi is dominated by arboreal non-flying mammals whose relative abundances are considerably higher than those of avian frugivores (Table 3). This is generally true for many undisturbed tropical wet forests (Gautier-Hion *et al.* 1985, Leighton & Leighton 1983, Terborgh 1983). However unlike other sites more than 80% (4/5) of the mammals were seed predators. This may be due to the large number of seeds produced compared to fleshy fruits as discussed earlier.

Among the mammals, giant squirrel and Nilgiri langur are territorial and sedentary (Borges 1993, Oates *et al.* 1980). While the giant squirrel was solitary but highly frugivorous, Nilgiri langur lived in groups but relying less on fruits; both had small home ranges compared to the lion-tailed macaque which ranged *c.* 5 km^2 (Borges 1993, Green & Minkowski 1977, Oates *et al.* 1980). Apart from fruits the lion-tailed macaque also consumes flowers of many species and flowers of *Cullenia exarillata* form an important resource for the monkeys at this site (Ganesh & Davidar 1997) and even elsewhere in the Anamalais (Menon 1993). However, the consistent sighting of lion-tailed macaques in 1993 was probably due to the greater amount of fleshy fruits (bird fruits) available which are their major food resource (Menon 1993). The high variance in sightings of lion-tailed macaque in Kakachi could have been due to the lack of continuous fleshy fruit supply in this habitat, besides the bigger troop size and frugivorous dietary preferences might have led to selection of a bigger home range comprising various vegetation mosaics subtly differing in tree species composition and possibly phenological trends. Such subtle differences of species composition in adjacent forests have been identifed in Kakachi (R. Ganesan; unpubl. data.).

The relationship between fruits and frugivores is often loose and non-obligate (Wheelwright & Orians 1982). Although one-to-one relationships do not exist in Kakachi, the reliance of the tree species on a frugivorous guild, which is neither very diverse nor abundant, makes their relationship extremely important. The Agasthyamalai mountain range, where this study has been conducted, harbours the largest unfragmented patch of forest in the Western Ghats (Ramesh *et al.* 1997) and this study is representative of fruit–frugivore interactions in such intact forest ecosystems. From the perspective of biodiversity conservation, the preservation of Kakachi forest becomes crucial as fragmentation might lead to decline of large frugivores such as the pigeons which in turn could lead to possible adverse effects on the recruitment of the large-seeded species dispersed by them. In addition, the disturbance of any single patch could affect *M. silenus* populations as they range between patches that are an integral part of the series of vegetation mosaics. Such considerations in the management of nature reserves in the Western Ghats need to be strongly advocated.

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