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Figs, Malabar Giant Squirrels, and Fruit Shortages Within Two Tropical Indian Forests[1]

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ABSTRACT

The role of figs as a resource for Malabar Giant Squirrels (*Ratufa indica*) during fruit shortages was investigated in two tropical forests in India. In general, figs were consumed to the greatest extent during lean fruiting periods, yet there was considerable intersquirrel variation in fig consumption during those periods. The importance of figs for a solitary, territorial, sedentary species such as the Giant Squirrel at these sites is limited only to those individuals who have access to figs within their territories or feeding ranges. The low density and spatial clumping of figs and the small number of fig species at the sites contributed to this phenomenon. The densities of figs were comparable to those found in other tropical areas. During fruit shortages figs may be an important resource only for a section of a frugivore population. Nutrient values of figs relative to other resources are also discussed.

Key words: *figs; frugivory; India; keystone species; Malabar Giant Squirrel; seasonality.*

In a recent paper Gautier-Hion and Michaloud (1989) examined the suggestion of Terborgh (1983, 1986a, 1986b) that figs are important key resources for both Neotropical and Paleotropical frugivorous vertebrates during periods of general annual fruit scarcity. This suggestion stemmed from the findings that figs were important in the lean season diets of several arboreal primates, procyonids, and birds in a Peruvian rain forest (Terborgh 1983) as well as from observations of a frugivorous community in a tropical lowland rain forest in East Kalimantan, Indonesia (Leighton & Leighton 1983).

The data from Gabon, West Africa, revealed that figs could not sustain most populations of frugivorous animals during lean fruiting periods and were probably important only to widely ranging species (Gautier-Hion & Michaloud 1989). Some species of Myristicaceae and Annonaceae were better suited to the role of key lean season fruit resources at this site.

Hypotheses about the role and identity of keystone fruiting species during lean fruiting periods can at present be evaluated at only a few sites with current data. This paper provides additional data on the relative importance of figs for Paleotropical frugivores during fruit shortages by focusing on a prominent arboreal frugivore of the Indian tropics—the Malabar Giant Squirrel (*Ratufa indica,* Sciuridae). This squirrel is a large, arboreal, solitary, territorial, facultative frugivore that switches to a diet of leaves (young and mature), flowers, and bark during periods of fruit scarcity (Borges 1989).

STUDY SITES AND METHODS

I observed the Malabar Giant Squirrel (*Ratufa indica*) in the Western Ghats of India within a semievergreen forest (Magod, Yellapur Reserve Forest, North Kanara District, Karnataka State; 74°45′E, 14°51′N; altitude 665 m) and in a moist evergreen seasonal cloud forest (Bhimashankar Wildlife Sanctuary, Pune District, Maharashtra State; 73°32′E, 19°4′N; altitude 900 m) for a period of 9 mo (January through September 1985) and 6 mo (January through June 1986), respectively (Borges 1989). The Magod site was dominated by *Terminalia tomentosa* (Combretaceae), *T. paniculata, Aporosa lindleyana* (Euphorbiaceae), and *Olea dioica* (Oleaceae). The Bhimashankar site was a forest in the Bhima river valley dominated by *Mangifera indica* (Anacardiaceae) and *Memecylon umbellatum* (Melastomataceae). Bhimashankar was fog bound from July through September and no data were collected during that time. Both sites receive seasonal monsoon rains from June through September. Annual rainfall at Magod and Bhimashankar during the year of the study was 1818 mm and 3922 mm, respectively. The rainfall at Magod during 1985 was lower than the previous 10-yr average of 2518 ± 459 mm.

At each site an area of approximately 22 ha was partitioned into a grid by trails at 50 m intervals. A smaller core area within this grid was selected

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for observation of focal animals. Focal animals were selected at random from a set of individually identifiable animals within the core observation area (15 and 18 animals at Magod and Bhimashankar, respectively). Each month the activities of approximately ten individual focal animals were continuously recorded from nest exit at dawn to nest entry at dusk, a single animal being followed on each observation day. The total number or total volume (in case of bark) of food items consumed per individual squirrel per day was obtained by actual counts and by estimations from feeding rates. Total and percent contributions (wet mass basis) of each food item and each food species to the daily diet were then calculated from the average wet masses of the food items.

Areas of 6.50 ha at Magod and 5.25 ha at Bhimashankar, which included the territories of focal animals, were demarcated for phenology studies. The fruiting phenology of all upper and middle story trees in these observation areas was recorded every month (1761 trees at Magod and 1878 trees at Bhimashankar) by counting the number of individuals bearing ripe fruit. Fruit crop size was not estimated. Squirrels rarely fed on shrubs and their phenology was therefore ignored. The position of all mature fig trees was mapped to the nearest 0.5 m.

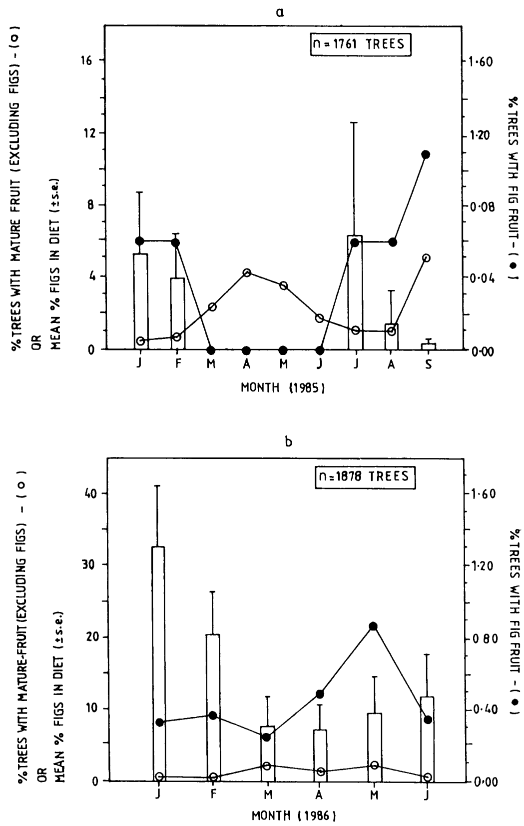

FIGURE 1. Monthly percent of trees in core study area with mature fruit (excluding figs) (O) and with fig fruit (●), and the mean monthly percent (±SE) of figs in the daily diet (wet mass basis). (a) Magod: *N* = total number of trees observed = 1761; number of squirrels observed each month: J = 9, F = 9, M = 9, A = 10, M = 10, J= 10, J = 10, A = 5, S = 11. (b) Bhimashankar: *N* = total number of trees observed = 1878; number of squirrels observed each month: J = 9, F = 10, M = 10, A = 10, M = 10, J = 10.

RESULTS

At both sites fruit was abundant from March to June. At Magod, fruit availability was low from January through February and from July through August. A fruit shortage occurred at Bhimashankar from January through February and in June (Figs. 1a and 1b).

At Magod the most important fruit resources (average representation in daily diet during fruit abundances >10%) were *Holigarna arnottiana* (Anacardiaceae) (23.8%), *Aporosa lindleyana* (20.5%), and *Artocarpus hirsutus* (Moraceae) (11.5%). At Bhimashankar the most important resource was *Mangifera indica* (33.1% of daily diet).

Figs were available at low levels only during fruit shortages at Magod and throughout the study period at Bhimashankar (Figs. 1a and 1b). At Magod, only one species of terrestrial fig (*Ficus tsjahela* N. Burman) occurred in the core area. Individuals of this species are large, deciduous trees. Of the 10 individuals present (1.54 per ha) only 4 fruited during the study period. This species fruited in 5 out of the 9 observation months in the core area. At Bhimashankar, two species of terrestrial figs occurred in the core area—*F. glomerata* Roxb. (syn. *F.* racemosa *L.*) (16 trees, 3.04 trees per ha) and *F. callosa* Willd. (8 trees, 1.52 per ha). *Ficus glomerata* is a medium-sized tree while *F. callosa* is a large tree often reaching the canopy. Both species were in fruit throughout the 6 mo observation period.

Despite the fact that figs were available during fruit shortages at both sites (a necessary criterion for a keystone resource), some squirrels were never observed eating figs; whereas, others fed extensively on them. This is indicated by the large variation around the monthly average values of daily fig consumption (Figs. 1a and 1b). The number of focal squirrels recorded feeding on figs each month ranged from 0 to 4 at Magod and from 0 to 5 at Bhi-

TABLE 1. *Monthly minimum and maximum contributions of figs to the daily diet of* Ratufa indica *(percent wet mass basis).*

Magod (1985)

Month	*Ficus tsjahela* Minimum	Maximum	N_1	N_2
Jan	0.0	32.3	4	9
Feb	0.0	18.5	3	9
Mar	0.0	0.0	0	9
Apr	0.0	0.0	0	10
May	0.0	0.0	0	10
Jun	0.0	0.0	0	10
Jul	0.0	63.1	1	10
Aug	0.0	7.8	1	5
Sep	0.0	3.3	1	11

Bhimashankar (1986)

Month	*Ficus glomerata*			*Ficus callosa*			
	Minimum	Maximum	N_1	Minimum	Maximum	N_1	N_2
Jan	0.0	50.4	3	0.0	73.4	5	9
Feb	0.0	53.1	2	0.0	36.0	4	10
Mar	0.0	40.7	3	0.0	11.3	5	10
Apr	0.0	25.6	3	0.0	5.3	3	10
May	0.0	50.1	4	0.0	8.1	1	10
Jun	0.0	23.1	3	0.0	52.1	2	10

N_1 = number of focal squirrels feeding on figs each month.
N_2 = number of focal squirrels observed each month.

mashankar (Table 1). At Magod, only 6 out of 15 focal squirrels were observed to eat figs. At Bhimashankar, *F. glomerata* was consumed by only 6 and *F. callosa* by only 8 of the 18 focal squirrels. Moreover, when maps of squirrel territories were superimposed on the distribution of *F. tsjahela* at Magod and of *F. glomerata* and *F. callosa* at Bhimashankar, it was evident that access to figs was impossible for some squirrels (N = 9 out of 15 focal animals at Magod, *i.e.,* 60%; N = 10 out of 18 focal animals at Bhimashankar, *i.e.,* 55.5%; maps available in Borges 1989). Moreover, *F. glomerata* is a riverine fig and was available only to those squirrels (N = 6, *i.e.,* 33.3% of focal animals) with territories adjacent to the Bhima river. Some individual squirrels at Bhimashankar had access to both species of figs (3 squirrels); whereas, others had access to only a single species (8 squirrels). It appears then that figs were important lean fruiting season daily resources only for some individual squirrels.

Figs were consumed to the greatest extent during lean fruiting periods. The recorded maximum contribution of figs to a squirrel's daily diet at Magod (63.1% wet mass) occurred in July which was a lean fruiting period (Table 1, Fig. 1a). The maximum contribution of figs to the daily diet at Bhimashankar—73.4% for *F. callosa* and 53.1% for *F. glomerata*—occurred in January and February which were also lean fruiting periods at Bhimashankar (Table 1, Fig. 1b). At Bhimashankar, the monthly means of daily fig consumption were 32.4 percent during fruit shortages and 7.4 percent during fruit abundances.

Fruit resources other than figs were extremely scarce during some months at both sites. For example, within the core area at Magod in January, only a single *Xylia xylocarpa* (Fabaceae), 5 *T. tomentosa* and one *Flacourtia montana* (Flacourtiaceae) bore fruit. At Bhimashankar, January and February were months of extreme fruit shortage with only 3 individuals of *Diospyros sylvatica* (Ebenaceae) and one *Xantolis tomentosa* (Sapotaceae) fruiting in the intensive study area besides figs. During these months, figs were the only fruit consumed, except one squirrel in January who consumed mature seeds of *X. tomentosa* (4% of daily diet). The average monthly consumption of fig fruit and of other fruit species is presented in Tables 2 and 3.

DISCUSSION

Two main characteristics determine the importance value of figs to frugivores during fruit shortages. The fruiting patterns of figs exhibit spatiotemporal

TABLE 2. *Contribution of fruit species to daily diet at Magod during months when figs were also consumed (percent wet mass: monthly mean and standard deviation) 1985.*

January		February		July		August		September	
FITS[a]	5.2 ± 10.6	APLI	19.3 ± 21.7	HLAR	26.7 ± 35.6	VIAL	5.7 ± 6.0	VIAL	48.8 ± 16.6
FLMT	0.9 ± 2.5	BULA	5.2 ± 10.7	GNUL	12.7 ± 13.6	FITS	1.5 ± 3.5	CASP	1.9 ± 3.5
		FLMT	4.2 ± 3.4	FITS	6.3 ± 20.0	TRCN	1.3 ± 2.9	RADM	0.6 ± 2.1
		FITS	3.9 ± 7.4	VIAL	2.9 ± 7.5			FITS	0.3 ± 1.0
		ALSE	2.2 ± 6.7	TRCN	1.0 ± 3.0				
		ARHI	1.4 ± 2.2	TETM	0.7 ± 1.3				

[a] Four letter code indicating fruit species: ALSE = *Alseodaphne semicarpifolia* (Lauraceae); APLI = *Aporosa lindleyana* (Euphorbiaceae); ARHI = *Artocarpus hirsutus* (Moraceae); BULA = *Buchanania lanzan* (Anacardiaceae); CASP = *Casearia esculenta* (Flacourtiaceae); FITS = *Ficus tsjahela* (Moraceae); FLMT = *Flacourtia montana* (Flacourtiaceae); GNUL = *Gnetum ula* (Gnetaceae); HLAR = *Holigarna arnottiana* (Anacardiaceae); RADM = *Randia dumetorum* (Rubiaceae); TETM = *Terminalia tomentosa* (Combretaceae); TRCN = *Trichilia connaroides* (Meliaceae); VIAL = *Vitex alata* (Verbenaceae).

TABLE 3. *Contribution of fruit species to daily diet at Bhimashankar during months when figs were also consumed (percent wet mass: monthly mean and standard deviation) 1986.*

January		February		March		April		May		June	
FICA[a]	24.8 ± 28.5	FICA	11.4 ± 15.0	MAIN	27.2 ± 30.3	MAIN	22.9 ± 21.4	MAIN	26.7 ± 24.8	MAIN	64.7 ± 18.0
FIGL	7.6 ± 16.8	FIGL	8.8 ± 19.1	AMLA	6.3 ± 10.2	ELDI	16.0 ± 9.5	EUJA	9.4 ± 13.3	GATA	11.9 ± 12.8
				LIST	5.7 ± 12.1	AMLA	7.6 ± 13.5	FIGL	8.8 ± 16.1	FICA	8.0 ± 17.8
				FIGL	5.4 ± 12.7	FIGL	6.2 ± 10.5	DIMA	6.3 ± 7.2	FIGL	3.6 ± 7.9
				GNUL	2.3 ± 7.2	GNUL	5.5 ± 5.8	CABR	2.4 ± 7.3	EUJA	1.9 ± 3.2
				FICA	2.0 ± 3.6	ARJA	1.6 ± 5.1	GNUL	2.2 ± 3.3	AMLA	1.0 ± 1.9
				ELDI	1.9 ± 6.0	FICA	0.8 ± 1.7	FICA	0.8 ± 2.6		

[a] Four letter code indicating fruit species: AMLA = *Amoora lawii* (Meliaceae); ARJA = *Artocarpus heterophyllus* (Moraceae); CABR = *Carallia brachiata* (Rhizophoraceae); DIMA = *Diploclisia macrocarpa* (Meníspermaceae); ELDI = *Olea dioica* (Oleaceae); EUJA = *Syzygium cumini* (Myrtaceae); FICA = *Ficus callosa* (Moraceae); FIGL = *Ficus glomerata* (Moraceae); GATA = *Garcinia talbotii* (Clusiaceae); GNUL = *Gnetum ula* (Gnetaceae); LIST = *Litsea stocksii* (Lauraceae); MAIN = *Mangifera indica* (Anacardiaceae).

patchiness (Janzen 1979, Milton *et al.* 1982) ensuring that some individual figs are in fruit throughout the year within the habitat. Also, figs are usually present at low densities in forest ecosystems and individual trees are usually clumped (Heithaus & Fleming 1978, Gautier-Hion & Michaloud 1989). Owing to these characteristics, it appears that figs can be exploited as a major fruit source only by a mobile species with a large home range and with the ability to track fruiting figs in the habitat. This probably occurs in Neotropical squirrel monkeys (Terborgh 1983), African pteropodid bats (Bradbury 1977, 1981; Marshall & McWilliams 1982) or the bulbul *Ixonotus gustatus* in Gabon (Gautier-Hion & Michaloud 1989). All fig-consuming species studied so far have group living social systems and all conclusions on fig utilization patterns have been drawn at the level of the group or population. The present study on Giant Squirrels has shown that figs are not a lean fruiting season resource for those individuals of a species with fixed territories that are so small that figs are not included within their feeding areas.

A comparison between the two study sites showed that the importance of figs in the consumer's diet depends on the number of fig species in the community, their availability on a spatiotemporal scale relevant to the consumer species, and their availability relative to other fruit species within the fruit resource base of the consumer species. At Magod, which had only one fig species in the core area, figs appeared to be less important than at Bhimashankar in which two species of figs occurred. At Magod, figs were unavailable for 4 out of 9 mo within the core study area (6.5 ha), although they may have been fruiting elsewhere in the site. The species of figs at Bhimashankar had differing distributions. *Ficus glomerata* was a riverine fig with a clumped distribution, while *F. callosa,* although having a clumped distribution, was not restricted to any particular topographic area within the habitat (Borges 1989) and was also consumed by a greater number of squirrels than *F. glomerata*. The overall mean density of 1.5 individuals/ha for 20 species at Gabon (Michaloud & Michaloud-Pelletier 1987) is similar to the densities recorded for two of the three species at Magod and Bhimashankar. *Ficus glomerata* had a higher density of 3.0 individuals/ha. Squirrels at either site had an average daily feeding range of 0.4 ha (Borges 1989). Therefore the spatial scale of access can influence the temporal availability of such a resource to certain individuals of such a relatively sedentary consumer species.

The importance of figs as a resource during fruit shortages would also depend on whether figs are indeed available during fruit shortages, or whether they are available throughout the year but are consumed only during fruit shortages because they are less preferable than other fruit species. Both these situations occurred at the study sites. Figs were virtually the only fruit available at both sites in the early dry season (January through February) and in fact were the only fruit consumed at Bhimashankar in February. Unlike Magod, however, figs were available throughout the year at Bhimashankar. Yet, they were not as important in the diet as other fruit during periods of fruit abundances. This may be due to their lower nutritive value compared to other fruit, especially their levels of soluble carbohydrates (Table 4). The lignocellulose values of figs at both sites as measured by ADF (Acid Detergent Fiber) contents (see Borges 1992 for nutrient analysis methods) are also higher than that of other fruit (Table 4) indicating that figs are less digestible than other fruit resources. Low digestibility values were also observed in fig species in West Malaysia (Vellayan 1981). Borges (1989, 1992) has shown that the content as well as the rates of ingestion (search and handling times included) of soluble carbohydrates are important positive predictors of the relative consumption of food resources. The soluble carbohydrate level of the fig species at Magod as measured by total nonstructural carbohydrates (TNC) was much higher than the average value for fruit at that site, yet their rarity on a spatiotemporal scale probably precluded their overall importance in squirrel diets. At Magod, however, there was no significant difference between the TNC ingestion rate from *F. tsjahela* and that from other fruit species available at the same time (t-test, $P > 0.05$; Table 5). At Bhimashankar, the TNC ingestion rate from *F. callosa* was significantly lower than that from other fruit (t-test, $P < 0.001$), while that from *F. glomerata* was not significantly different from the value from other fruit (t-test, $P > 0.05$; Table 5).

Individuals without access to figs during fruit shortages consumed either other available fruit or resorted to a diet composed largely of fibrous nonfruit resources such as leaves, flowers, bark, and pith. For example, during the second fruit shortage at Magod, the average daily consumption of mature leaves was 42.2 percent of the daily diet, of bark was 8.3 percent and of pith was 6.5 percent. These values during the peak fruiting season in April were 15.0 percent for leaves, 1.2 percent for bark and 0 percent for pith (Borges 1989). During the one observed lean fruiting period at Bhimashankar, the average daily consumption of leaves was 24.4 per-

TABLE 4. *Nutrient contents of fig fruit compared to other concordantly available fruit and to nonfruit resources consumed by squirrels without access to figs (average percent wet mass ± standard deviations in gm). Analytical methods for all nutrients available in Borges (1989, 1992).*

	Magod				
	Ficus tsjahela	Other fruit	*N*	Nonfruit resources	*N*
Fat	0.84	8.25 ± 10.62	23	0.50 ± 0.32	9
Nitrogen	0.18	0.67 ± 0.70	21	0.54 ± 0.32	10
TNC[a]	4.01	1.61 ± 1.67	23	1.30 ± 1.20	10
ADF[b]	12.15	7.83 ± 5.76	18	12.46 ± 9.80	9

	Bhimashankar					
	Ficus callosa	*F. glomerata*	Other fruit	*N*	Nonfruit resources	*N*
Fat	2.42	0.82	3.03 ± 9.18	19	2.20 ± 1.80	7
Nitrogen	0.38	0.11	0.36 ± 0.38	19	0.64 ± 0.34	7
TNC[a]	0.54	1.02	1.90 ± 1.25	19	1.58 ± 1.00	7
ADF[b]	19.77	7.45	3.80 ± 4.50	17	13.41 ± 10.81	7

cent, of bark was 21.1 percent and of flowers was 33.9 percent. By contrast, during peak fruit abundance in May at Bhimashankar, the average consumption of leaves, bark, and flowers were 7.7 percent, 2.5 percent and 3.7 percent, respectively (Borges 1989). This flexible feeding strategy is probably facilitated by a digestive system capable of fermentation of structural carbohydrates (Borges 1992). Leighton and Leighton (1983) have also observed that foliage and bark were principal resources for several primates and squirrels including *Ratufa affinis* during fruit shortages in East Kalimantan, Indonesia.

Individual squirrels without access to figs during fruit shortages may be at a nutritional disadvantage compared to those individuals with access to figs. This can perhaps be assessed by comparing the nutritive values of figs to the average nutritive value of the nonfruit resources (young leaves, bark, and flowers) consumed by squirrels without access to figs during lean fruiting seasons. If the first lean fruiting season (January and February) at both sites is considered (Tables 4 and 5), then the following comparisons can be made. At Magod, the single fig species had higher fat and TNC values and lower nitrogen values than the nonfruit resources, while the ADF values were closely similar. At Bhimashankar, the higher TNC levels, higher TNC ingestion rates, and low ADF values of *F. glomerata* make it a more preferable fig than *F. callosa*. Both species of figs have lower or similar fat, nitrogen, and TNC contents than the nonfruit resources. However, at both sites the TNC ingestion rates from figs are significantly higher than from the nonfruit resources

TABLE 5. *Rates of ingestion of total nonstructural carbohydrates (TNC) (gm/sec) from figs, other concordantly available fruit and nonfruit resources consumed by squirrels without access to figs (means ± standard deviations).*

Magod		
Ficus tsjahela	$4.13 \times 10^{-4} \pm 7.05 \times 10^{-5}$	*N* = 10
Other fruit	$2.55 \times 10^{-4} \pm 3.26 \times 10^{-4}$	*N* = 114
Nonfruit resources	$1.75 \times 10^{-4} \pm 1.51 \times 10^{-4}$	*N* = 81
Bhimashankar		
Ficus callosa	$4.47 \times 10^{-4} \pm 1.26 \times 10^{-4}$	*N* = 20
F. glomerata	$8.20 \times 10^{-4} \pm 3.43 \times 10^{-4}$	*N* = 10
Other fruit	$7.39 \times 10^{-4} \pm 5.50 \times 10^{-4}$	*N* = 139
Nonfruit resources	$1.24 \times 10^{-4} \pm 5.63 \times 10^{-5}$	*N* = 187

N = sample size = ingestion rate per food item per focal squirrel per day calculated as an average value per item per day.

(t-tests, $P < .001$; Table 5). Therefore, from the point of view of the rates of ingestion of important nutrients such as soluble carbohydrates, figs are preferable to resources such as bark, leaves, and flowers. Individuals without access to figs may, therefore, be at a disadvantage in terms of feeding on resources from which they can obtain these important nutrients at a lower feeding rate and, therefore, at perhaps a higher feeding cost. It appears, therefore, that more attention needs to be paid to the relative nutritional benefits of key resources during lean fruiting periods.

Figs may be important to other frugivores in these systems but probably more so for the nomadic or migratory species as also found by Leighton and Leighton (1983), Terborgh (1983), Robinson (1986), and Gautier-Hion and Michaloud (1989). I did not collect systematic data on visitation to fig trees by frugivores other than *Ratufa*. However, at Magod the largest frugivorous birds such as Grey-fronted Green Pigeons (*Treron pompodora*), Imperial Pigeons (*Ducula badia*), Malabar Grey Hornbills (*Tockus griseus*), Malabar Pied Hornbills (*Anthracoceros coronatus*), and Great Indian Hornbills (*Buceros bicornis*) were regularly observed at fig trees. Occasionally, the small, omnivorous Three-striped Palm Squirrel (*Funambulus palmarum*) was observed feeding on figs. At Magod, Giant Squirrels fed on the massive fig crops of *F. tsjahela* simultaneously with frugivorous birds. However at Bhimashankar, no other vertebrate species was observed feeding with squirrels in fig trees. The Malabar Grey Hornbill is a migratory visitor to Bhimashankar and was observed within the study site only when large fruit crops of *F. callosa* were available. Primates were not important fig consumers at these sites. The common langur (*Presbytis entellus*) was not observed eating figs at Magod and was only observed eating *F. callosa* on a few occasions at Bhimashankar. The only other primates at the sites were the rhesus macaque (*Macaca mulatta*) and the bonnet macaque (*M. radiata*). Neither species was observed consuming figs. No data are available for fig consumption by bats nor for other nocturnal frugivores such as civets (Viverridae). The one species of flying squirrel (*Petaurista petaurista*) that occurred at Magod is probably largely folivorous (Muul & Liat 1978). It is possible, therefore, that at two sites in India also, figs could serve as key resources during fruit shortages for only wide ranging, locally migrating species of a frugivorous community.

The present study shows that individuals of fig-consuming species with sedentary, territorial lifestyles may vary in their dependence on figs during general annual fruit shortages. The importance value of figs during lean fruiting periods for individuals of such species is subject to a variety of spatiotemporal factors all of which have to be independently evaluated. Keystone resources may not serve the whole population of certain frugivore species. Moreover, the nutritional profiles of key resources relative to other available fruit and nonfruit resources need to be considered in order to evaluate their overall importance to frugivore populations.

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