15. Jie He, Huang, Lin-Ke, Chow, W. S., Whitecross, M. I. and Anderson, J. M., *Aust. J. Plant Physiol.*, 1993, **20**, 129–142.
16. Li, J., Ou-Lee, T. M., Raba, R., Amundson, R. G. and Last, R. L., *The Plant Cell*, 1993, **5**, 171–179.
17. Teramura, A. H. and Sullivan, J. H., *Photosynth. Res.*, 1994, **39**, 463–473.
18. Teramura, A. H., Biggs, R. H. and Kossuth, S., *Plant Physiol.*, 1980, **65**, 483–488.
19. Reid, D. M., Beallard, F. D. and Pharis, R. P., in *Plant Physiol: A Treatise, Growth and Development* (ed. Bidwell, R. G. S.), Academic Press, San Diego, 1991, pp. 65–181.
20. Jansen, M. A. K., Gava, V., Greenberg, B. M., Mattoo, A. K. and Edelman, M., *The Plant J.*, 1996, **5**, 693–699.
21. Hu, M. L. and Tappel, A. L., *Photochem. Photobiol.*, 1992, **56**, 357–363.
22. Beggs, C. and Wellman, E., *Photochem. Photobiol.*, 1985, **41**, 481–486.
23. Okamura, N., Haraguchi, H., Hashimoto, K. and Yagi, A., *Phytochemistry*, 1994, **5**, 1463–1466.
24. Tevini, M. and Steinmuller, D., *J. Plant Physiol.*, 1987, **131**, 111–121.
25. Hahlbrook, K. and Scheel, D., *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 1989, **40**, 347–369.
26. Robberecht, R. and Caldwell, M. M., *Oecologia*, 1978, **32**, 277–287.

Received 28 March 1996; revised accepted 7 February 1997

Temporal patterns of visitation among avian frugivores at fruiting strangler figs in a tropical evergreen forest in the Western Ghats, Southern India

Vidya R. Athreya

National Centre for Radio Astrophysics, Post Bag 3, Pune University Campus, Pune 411 007, India

Frugivory observations were conducted at fruiting strangler figs in Karian Shola National Park in the Anaimalai hills from January to March 1993. A total of 123 hours of fruit use by frugivores was observed at fruiting trees of four species of *Ficus*. Frugivore activity was seen throughout the day with a major peak in visitation between 7.00 AM and 9.30 AM and a minor one at 2.30 PM. The common frugivore species exhibited preferences for different species of fruiting strangler figs, occurring in larger numbers at these trees. Of the seven common species of avian frugivores, only two pairs exhibited similar temporal patterns of visitation to the fruiting strangler figs, the Small Green Barbet–Crimsonthroated Barbet pair at *F. drupacea* and bulbul spp.–Golden Oriole pair at *F. microcarpa*. The pressures of competition, past or contemporary may be the reason behind the difference in the temporal pattern of visitation. However, it is unlikely that active competition is the cause since very few inter-specific aggressive interactions were noted. What is unclear is the similar temporal pattern of visitation in the case of the bulbul spp.–Golden Oriole pair at *F. microcarpa*, their preferred tree and the barbet pair at *F. drupacea*, not their preferred tree.

FRUITING fig trees, especially those that are bird-dispersed, attract avian frugivores in large numbers[1]. This has led to a number of studies on frugivore composition and their interactions at this superabundant fruit resource[2–6]. Visitations to the fruiting trees may depend on physiological needs of the frugivores and the local factors peculiar to each fruiting tree. Time spent by a frugivore at a fruiting tree would depend on its nutritional needs, diet and activity budgets. The presence of predators and the interactions among the frugivores could also affect visitation rates[7,8]. Kantak[7] surmised that the different visitation patterns of the common frugivores could be due to interference competition. This paper presents the results from a study of temporal partitioning of the fruit resource among avian frugivores visiting fruiting strangler figs in a tropical evergreen forest in the southern Western Ghats, India. The null hypothesis of no differences in the temporal patterns of visitation was tested against the alternative hypothesis of temporal partitioning of the fruit resource by the common frugivores.

The study was conducted from 21 January to 31 March 1993, at Karian Shola National Park in the Indira Gandhi Wildlife Sanctuary, Pollachi district, Tamil Nadu, India. The Karian Shola National Park (10°27'N, 76°51'E; altitude c. 765 m) is spread over 506 ha of tropical evergreen forest. It is contiguous with similar forest across the Kerala–Tamil Nadu border in the Parambikulam Wildlife Sanctuary. It is classified as the west coast tropical evergreen forest with the characteristic tree species being *Hopea parviflora* and *Messua ferrea*[9]. The national park is surrounded by moist deciduous forests and teak plantations. Most of the precipitation in this region occurs during the south-west monsoon (from June to August) but the effect of the north-east monsoon (during November and December) is also felt. This area received 1778.2 mm of rain in 1992 and 27.8 mm during the three-month study period.

A total of 123 hours of frugivory observations was conducted at three trees of *Ficus drupacea* (67 h), one tree of *F. microcarpa* (40 h) and two trees of *F. amplissima* (16 h). Observations were conducted between 7.00 AM and 5.00 PM. The bird species and their numbers were noted during every alternate 5-minute period.

The trees chosen for observations had to satisfy certain criteria. They had to have large synchronously ripening fruit crops; usually bird-dispersed fruiting characteristics in the old world tropics[1]. The trees had to be relatively shorter and located in more open areas. In

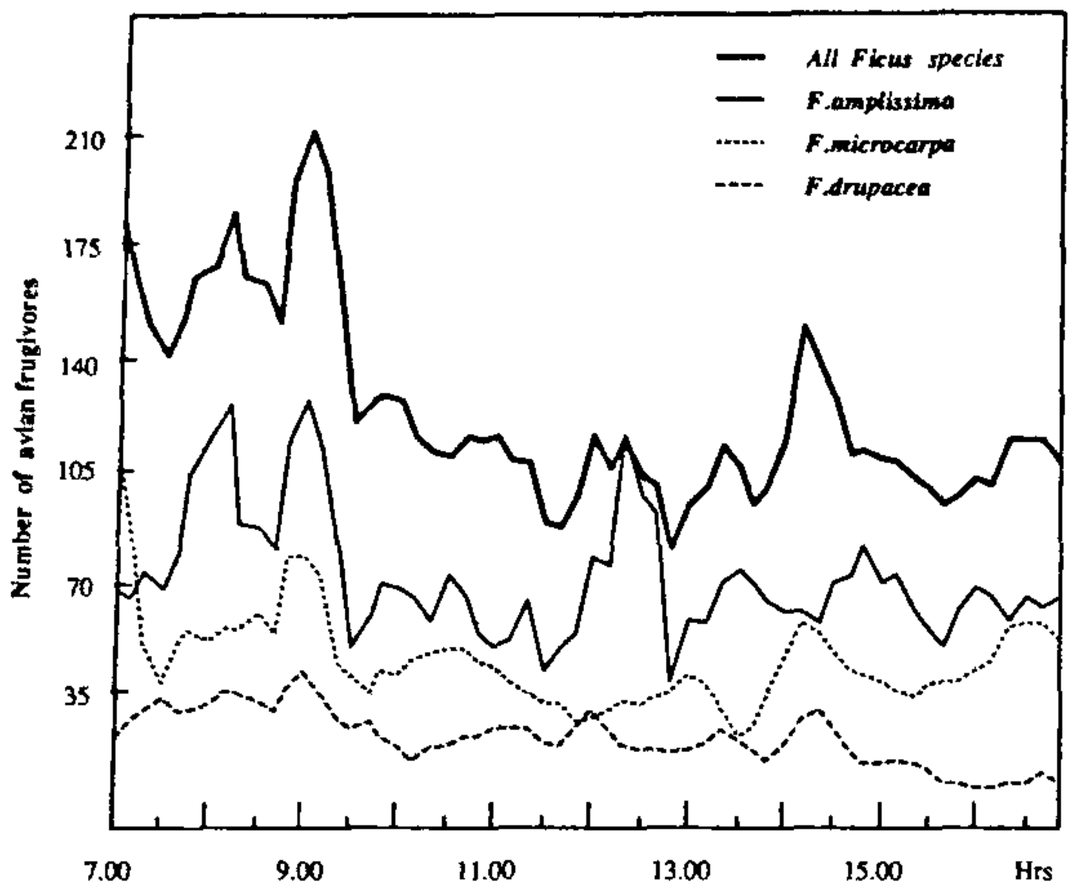

Figure 1. Temporal pattern of visitation of avian frugivores at fruiting *Ficus* trees through the day. The data presented here represent a four-day aggregate of the number of avian frugivores visiting the three *Ficus* species and a 13-day aggregate for all the *Ficus* species combined.

addition, the foliage density had to be low. This was essential to facilitate the identification of important frugivores like the Greyfronted Green Pigeons (*Treron pompadora*) and barbets (*Megalaima* spp.) which are small and green in colour and to obtain a reasonably accurate count of birds in general. This strongly constrained the number of trees that could be observed. Most of the sampled trees were present on the edges of clearings and in riparian areas within the evergreen forest.

Although these trees were chosen based on the above criteria, it is unlikely that this selection would have in any way affected the visitation of the birds both in terms of species as well as numbers to the trees. This is corroborated by the fact that despite the difference in the number of hours of observation at each species of *Ficus*, the number of frugivore species recorded was around the same (19 species were recorded at *F. amplissima*, 24 *F. drupacea* and 26 at *F. microcarpa*). Also, the seven common species that have been used for analysis of frugivore visitation pattern were recorded in fair numbers at all three *Ficus* species[10].

The visitation patterns of all the avian frugivores were studied through the day. For analysis of differences in temporal patterns of visitation, seven of the most common frugivores namely Malabar Grey Hornbill (*Tockus griseus*), Greyfronted Green Pigeon (*Treron pompadora*), Small Green Barbet (*Megalaima viridis*), Crimsonthroated Barbet (*M. rubricapilla*), the bulbuls (*Pycnonotus melanicterus gularis, P. jocosus* and *Hypsipetes indicus*), Golden Oriole (*Oriolus oriolus*) and Fairy Bluebird (*Irena puella*) were considered. The three species of Pycnonotidae were grouped together to improve the statistics as the visitation frequencies of the individual species were low. If the patterns of visitation of the three species were different, their combined data would have yielded smoother pattern. However, the combined data show a definite periodic pattern in their visitation which justifies the assumption that the visitation patterns of the three species are similar.

The number of days during which observations were conducted was not the same for all the time intervals between 7.00 AM and 5.00 PM. The bird numbers in each interval have been scaled to the median value of 13 days to analyse the temporal patterns across a day. The analysis was repeated for each of the three strangler fig species. The bird numbers were smoothened by taking an average over three successive time intervals.

A multinomial χ^2 goodness of fit test was employed to check the null hypothesis of no differences in the patterns of visitation of the common frugivores, taken a pair at a time. In order to improve the reliability of the χ^2 statistic, two constraints were imposed during analysis. Only those time intervals in which the expected number of birds was greater than 2.0 were considered. This severely reduced the number of usable time intervals, especially when the data from different *Ficus* species were considered separately. This in turn resulted in inordinately high values of significance for the null hypothesis which was in fact an artifact due to bad statistics. To avoid this artifact, only the results of those bird pairs which had at least 30 usable time intervals in common (out of a maximum of 60 through the day) have been considered[11].

The fruiting strangler figs had a continuous stream of frugivores right through the day with a major peak in frugivore activity between 7.00 AM and 9.30 AM and a much smaller one at around 2.30 PM (Figure 1). The pronounced early morning peak in frugivore activity may have been due to the increased food requirements of the frugivores at the start of a day. It seems likely then, that there will be another peak in frugivore activity at the fruiting strangler figs at the end of the day, before the frugivores turn in for the night.

The avian frugivores preferred different species of *Ficus*, occurring in large numbers at these species (Table 1). The Malabar Grey Hornbill preferred *F. drupacea*, the Green Pigeons and the barbets preferred *F. amplissima* while the bulbuls, Golden Orioles and Fairy Bluebirds showed a preference for *F. microcarpa*. It is well known that bird-dispersed figs when ripe are harvested by various size of birds, since even those with smaller gape sizes can eat the soft fruit by pecking out small pieces[12]. However, in terms of optimal utilization of the food resource, it is likely that a frugivore will try to eat the largest possible fig convenient given its gape size rather than ingest smaller figs or take bites of larger figs. We see such a trend here with the Malabar Grey Hornbill, the largest of the frugivores preferring the large fruits of *F. drupacea* (1.5–2.0 cm across[13]) while

Table 1. Mean number of avian frugivores at fruiting *Ficus* trees

	Mean number of birds/10 min interval								Mean of days observed
	MGH	GP	SGB	CTB	BUL	FBB	GO	TOT	
Total	0.80	1.79	1.01	2.40	0.78	0.32	0.89	9.47	13
F. amplissima	0.06	3.88	2.47	10.17	0.30	0.00	0.09	18.05	2
F. drupacea	1.11	0.77	0.64	1.48	0.18	0.15	0.04	5.45	7
F. microcarpa	0.38	2.65	0.85	0.61	1.74	0.58	2.50	11.14	4

MGH, Malabar Grey Hornbill; GP, Greyfronted Green Pigeon; SGB, Small Green Barbet; CTB, Crimsonthroated Barbet; BUL, Bulbul spp.; FBB, Fairy Bluebird; GO, Golden Oriole; TOT, Sum of all the avian frugivores.

Table 2. The p-values from the χ^2 test of the null hypothesis of no temporal variation in visitation of pairs of common avian frugivores

Birds species	MGH	GP	SGB	CTB	BUL	GO	FBB
MGH	(626)			*Combined data from all trees.*			
GP	<0.005	(1401)				*df* = 59	
SGB	<0.005	<0.005	(792)				
CTB	<0.005	<0.005	ns	(1878)			
BUL	<0.005	<0.005	= 0.03	= 0.095	(611)		
GO	<0.005	<0.005	<0.005	= 0.017	ns	(699)	
FBB	insf.data	insf.data	insf.data	insf.data	insf.data	insf.data	(251;

Bird species	GP	SGB	CTB
			F. amplissima
GP	(446)		*df* = 59
SGB	insf.data	(297)	
CTB	<0.005	<0.005	(1221)

Bird species	GP	BUL	GO
			F. microcarpa
GP	(638)		*df* = 59
BUL	<0.005	(418)	
GO	<0.005	ns	(600)

Bird species	MGH	GP	SGB	CTB
MGH	(467)			*F. drupacea*
GP	<0.005	(324)		
	df = 47			
SGB	<0.005	insf.data	(272)	
	df = 53			
CTB	<0.005	<0.005	ns	(622)
	df = 56	*df* = 54	*df* = 57	

The numbers within parentheses are the sample sizes of the corresponding birds. MGH, Malabar Grey Hornbill; GP, Greyfronted Green Pigeon; SGB, Small Green Barbet; CTB, Crimsonthroated Barbet; BUL, Bulbul spp.; GO, Golden Oriole; FBB, Fairy Bluebird; ns, not significant (>0.1); *df*, degrees of freedom; insf.data, insufficient data.

the bulbuls preferred *F. microcarpa* which has the smallest fruits among the three *Ficus* species.

Excepting two pairs, all the 21 possible pairings of the seven most common frugivores exhibited differing temporal patterns of visitation at the fruiting strangler figs (Table 2). Kantak[7] recorded a similar result at five species of fruiting trees, including a *Ficus* species. The only two pairs which did show similar temporal patterns in visitation were the Small Green Barbet–Crimsonthroated Barbet pair at *F. drupacea* and the bulbul spp.–Golden Oriole pair at *F. microcarpa*. The reasons for the similarity in temporal visitations shown by these pairs of frugivores are not clear. What is puzzling is that while the barbet pair exhibited similar temporal pattern of visitation at a tree which was not their preferred species, the bulbul spp.–Golden Oriole pair exhibited similar visitation pattern at their preferred tree.

One could argue that at their preferred tree, the higher pressures the barbets face from the members of other congeneric species has led to the temporal partitioning of the resource. Therefore at *F. drupacea*, which is not their preferred tree and where competition from the other barbet species is likely to be lower, the closely related barbets have similar patterns of visitation. However, the bulbul spp.–Golden Orioles pair neither have similar habits nor are they closely related[14] to explain the similarity in their visitation pattern to their preferred tree.

The reasons given for temporal variations are many[7,8,15]. Predation pressures and aggression were certainly not the major reasons at Karian Shola National Park as very few instances of predatory attempts (seven in 123 hours of which none were successful) and interspecific aggression (seven in 56 hours of observation) were seen among the birds[10]. While figs are a superabundant resource, they are almost completely utilized by the frugivores[10] and one would expect competition over the resource. Perhaps past competition has moulded present frugivore behaviour and resource partitioning, and manifested in differing patterns of temporal visitations among frugivores.

In conclusion, the fruiting *Ficus* trees were host to frugivores throughout the day, with a higher activity in the early morning and mid afternoon. The major peak in the early morning could be explained by the increased food requirements of the frugivores who have started their day after a long gap in feeding. I would expect another peak in activity prior to sundown when the birds have to stock up for the night. The common frugivores occurred in larger numbers at certain species of *Ficus* and this preference is likely to be based on the optimal exploitation of a fig given the gape size of the frugivore. Most of the avian frugivores, including the two most common at each fruiting tree had differing temporal patterns of visitation to these super-abundant resources. Predation was rare and aggressive interactions between species very few which makes active interspecific competition an unlikely explanation for the differing patterns. What is difficult to explain is the similar temporal pattern of visitation of the bulbul spp.–Golden Oriole pair, at their preferred fruiting tree. Perhaps the biology and activity patterns of different species condition them to particular temporal patterns of behaviour.

1. Lambert, F. R. and Marshall, A. G., *J. Ecol.*, 1991, **79**, 793–809.
2. Brockelman, W. Y., *Nat. Hist. Bull. Siam Soc.*, 1982, **30**, 33–44.
3. Breitwisch, R., *Biotropica*, 1983, **15**, 125–128.
4. Coates-Estrada, R. and Estrada, A., *J. Trop. Ecol.*, 1986, **2**, 349–357.
5. Bronstein, J. L. and Hoffmann, K., *Oikos*, 1987, **49**, 261–268.
6. Lambert, F. R., *Ibis*, 1989, **131**, 521–527.
7. Kantak, G. E., *Condor*, 1981, **83**, 185–187.
8. Howe, H. F., *Am. Nat.*, 1979, **114**, 925–931.
9. Champion, H. G. and Seth, S. K., *Forest Types of India*, Govt. of India, Delhi, 1968.
10. Athreya, V. R., MS Thesis, University of Pondicherry, Pondicherry, 1993.
11. Hogg, R. V. and Tanis, E. A., *Probability and Statistical Inference*, Macmillan, New York, 1989.
12. Janzen, D. H., *Ann. Rev. Ecol. Syst.*, 1979, **10**, 13–51.
13. Matthew, K. M., *The Flora of Tamilnadu Carnatic*, Diocesan Press, Madras, 1983.
14. Ali, S. and Ripley, S. D., *Compact Handbook of the Birds of India and Pakistan*, Oxford University Press, Delhi, 1986.
15. Fleming, T. H., *Am. Zool.*, 1981, **19**, 1157–1172.

ACKNOWLEDGEMENTS. I thank Dr. Priya Davidar for supervising this work, Ramana M. Athreya and R. Kannan for their help throughout the project, Ganeshan (Erumaparai village) for his help in the field and the Tamil Nadu Forest Department for granting permission to carry out this work. Part of this project was funded by BNHS, Bombay.

Received 1 March 1996; revised accepted 25 February 1997

Vegetational and climatic changes during recent past around Tipra Bank Glacier, Garhwal Himalaya

A. Bhattacharyya and M. S. Chauhan

Birbal Sahni Institute of Palaeobotany, Lucknow 226 007, India

Palynological studies from Tipra Bank Glacier, UP Himalaya indicate that the climate was warm moist, similar to today's, prior to 720 yr B.P. This then reverted to comparatively cold dry climate around 620 yr B.P. when the glacier might have descended down. The climate changed to warm moist regime again around 460 yr B.P.

PALYNOLOGICAL studies from glacial sediments above tree limit or alpine region of the Himalaya are limited in number[1–3]. Most of the studies on this aspect are confined to temperate and subtropical sites[4,5].

We have attempted here to understand the changes of vegetation around Tipra Bank Glacier and their relationship to glacial fluctuations using pollen data of both surface and subsurface sediments of near present day snout.

Tipra Bank Glacier (Figure 1), one of the major glaciers in Bhyundar Ganga valley of Alaknanda catchment, joins another major glacier, Rataban and together they form a common snout. Bhyundar Ganga river originates from this snout and flows through the famous Valley of Flowers and ultimately joins Alaknanda river at Govindghat near Pandukeshwar. There are fourteen other glaciers which are of small niche types. The detailed climatic data around the site is not available. A general observation in this regard indicates that the