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IDENTIFYING DIURNAL AND NOCTURNAL FRUGIVORES IN THE TERRESTRIAL AND ARBOREAL LAYERS OF A TROPICAL RAIN FOREST IN SRI LANKA

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Abstract. We recorded fruit consumption by birds and mammals at 15 large-fruited tree species in the Sinharaja rain forest in Sri Lanka. For each plant species, we placed piles of ripe fruits on the terrestrial and in the arboreal layer, and recorded visitations to these piles with automatic cameras over 24 hours a day; 1628 photographs revealed 23 animal species visiting the piles. Of these consumers, 42% were entirely arboreal and 37% entirely terrestrial; the remainder visited fruit piles on both the terrestrial and in the arboreal layer. Of the animal species, 48% visited the piles during the day and 52% at night. None visited during both day and night. These data highlight the necessity of studying both arboreal and terrestrial consumers at different times of day to document the entire frugivore assemblage at different tree species. Neglecting one set of consumers or one time of day might result in missing species that could prove to be important frugivores or seed dispersers. *Accepted 14 February 2007*.

Key words: *arboreal*, *camera traps*, *canopy*, *Sinharaja tropical rain forest*, *Sri Lanka*, *terrestrial*.

INTRODUCTION

Studies identifying consumers of fleshy fruits in tropical forests have made considerable advances in recent years (see Fleming 2005). However, with the exception of studies on bats, large rodents, and deer (e.g., bats: Utzurrum 1995, Banack 1998, Eby 1998, Hodgkison *et al*. 2003; rodents: Forget, 1992, 1993, 1996; deer: Bodmer 1991, Prasad *et al*. 2006), most have focused on diurnal animals in the arboreal layer (e.g, birds and primates). As a result, studies of nocturnal and terrestrial animals are rare in comparison. Fruit consumers in tropical forests occupy both the arboreal and terrestrial layers, and can be diurnal or nocturnal. Few attempts have been made to understand these animal communities, their use of different layers in the forest, and their activity patterns.

While frugivore assemblages in Asia and Africa have been either studied during the day or the night or on arboreal or terrestrial levels, few studies have simultaneously compared frugivore assemblages over 24 hours and in both layers (Harrison 1962, Whitmore & Burnham 1984, Gautier-Hion *et al*. 1985, Van Schaik & Griffiths 1996, Miura *et al*. 1997, Hamann and Curio 1999, Engel 2000, Jayasekara *et al*. 2003, Bollen *et al*. 2004, Kitamura *et al*. 2002, 2004, 2006), and by employing the direct observation method (but see Van Schaik & Griffiths 1996, Miura *et al*. 1997, and Jayasekara *et al*. 2003). Even though direct observations allow a complete overview of animal visitors, there is a risk of missing out nocturnal and shy animals, due to the dense foliage and human disturbance. Van Schaik & Griffiths (1996), Miura *et al*. (1997), and Jayasekara *et al*. (2003) overcame these obstacles by using automatic cameras to record visits by terrestrial animals to fruiting trees. Among these studies, Miura *et al*. (1997) recorded some nocturnal animal species which were not before recorded in their study fields. Additionally, most studies of seed dispersal have been concentrated in Central and South, America and in Africa and a comparatively limited number have been carried out in Asia (e.g., Harrison 1962, Van Schaik & Griffiths, 1996, Miura *et al*. 1997, Corlett 1998, Hamann & Curio 1999, Jayasekara *et al*. 2003, Kitamura *et al*. 2002, 2004, 2006). Furthermore there exists, so far, only one study on aspects of frugivory in Sri Lanka (Jayasekara *et al*. 2003), so our present knowledge is almost negligible. However it is difficult to apply data from other

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TABLE 1. Study fruit species, their representation in the forest and fruit characteristics.

Family	Species	Layer	Experiment duration Days	Fruit type	Color	Fruit size mm (mean)	Seed size mm (mean)	Abbreviation
Anacardiaceae	*Mangifera zeylanica*	Sub canopy	26	Drupe	Green	31.9	26.29	MZ
	Semicarpus walkeri	Sub canopy	12	Drupe	Red	18.4	10.11	SW
Bombacaceae	*Cullenia rosayroana*	Sub canopy	22	Schizocarp	White	137	28	CR
	Cullenia ceylanica	Sub canopy	15	Schizocarp	White	64.5	20.78	CC
Clusiaceae	*Garcinia hermonii*	Sub canopy	15	Drupe	Green	40.4	13.32	GH
Ebenaceae	*Diospyros racemosa*	Sub canopy	12	Drupe	Green	27.9	15.22	DR
Euphorbiaceae	*Podadenia thwaitesii*	Sub canopy	14	Drupe	Green	41.6	17.62	PT
	Glennia unijuga	Sub canopy	15	Drupe	Green	25.2	19.61	GU
Meliaceae	*Dysoxylum ficiforme*	Sub canopy	21	Drupe	Brown	32.1	16.71	DF
	Walsura trifoliata	Sub canopy	16	Drupe	Brown	20.1	13.53	WT
Menispermaceae	*Coscinium fenestratum*	Liana	12	Drupe	Brown	23.6	17.09	CF
Moraceae	*Artocarpus nobilis*	Sub canopy	16	Compound	Brown	116.7	13.57	AN
Myristicaceae	*Horsfieldia iriya*	Sub canopy	25	Schizocarp	Orange	43.2	27.24	HI
	Myristica dactyloides	Sub canopy	26	Schizocarp	Orange	37.8	24.34	MD
Rosaceae	*Prunus walkeri*	Sub canopy	18	Drupe	Black	22.7	18.68	PW

studies to the Sri Lankan forest directly since, due to their long isolation, the fauna and flora of the island of Sri Lanka are different from continental India or any other land mass in the region. These concerns underscore the necessity of understanding the fruit-frugivore relationship in the Sri Lankan forest.

We used automatic cameras to monitor frugivore visits at 15 species of fruiting trees in a Sri Lankan rain forest. We recorded visits to piles of fruits placed in the arboreal and on the terrestrial layers, 24hours per day. The first goal of our study was to understand the frugivore assemblage in a 24-hour period in arboreal and terrestrial layers, and to recognize when and where the fruit species were consumed. A second goal was to evaluate the use of automatic cameras as a technique to describe frugivore assemblages.

METHODS

We worked in the Sinharaja tropical rain forest in Sri Lanka from June 2000 to January 2001 and July to December 2001. The Sinharaja forest is the largest undisturbed forest in Sri Lanka. It is a Man and Biosphere Reserve and is listed as a World Heritage Site (Gunatilleke & Gunatilleke 1996). The forest encompasses approximately 112 km^2 in southwestern Sri Lanka (Gunatilleke & Gunatilleke 1996). Mean annual temperature ranges from 19 to 31°C. Mean annual rainfall ranges from 3600 to 6000 mm, with distinct monsoonal peaks in May and November (Gunatilleke & Gunatilleke 1996). The vegetation is categorized as lowland tropical wet evergreen forest. It is dominated by species of Dipterocarpaceae, Clusiaceae, Sapotaceae, Bombacaceae, and Myrtaceae (Gunatilleke & Gunatilleke 1996).

A survey of woody species >30 cm dbh recorded 211 species, belonging to 119 genera and 43 families (Gunatilleke & Gunatilleke 1996). Among these species, 64% were endemic to Sri Lanka. Surveys of birds and mammals found 39 species of mammals and 147 of birds; eight mammals and 18 birds were endemic to Sri Lanka (Kotagama & Karunarathna 1983, Kotagama & Fernando 1994).

Because we were especially interested in mammals and large birds, we selected plant species with large-seeded fleshy fruits (≥ 2 cm in diameter). Fruit and seed size and accessibility of these species are provided in Table 1. Fourteen species were trees between 20–35 m in height and belonging to ten families (Table 1). One species (*Coscinium fenestratum*) was a vine. To set the cameras, we selected two plants of each species that had large, fully ripened fruit crops. On the other hand, we did not use two individuals of the same plant species with fully ripened fruit crops in close vicinity in order to avoid visits by the same animals. Therefore the minimum distance between individuals was chosen to be more than one kilometer.

To identify animals visiting the fruiting trees we used film cameras with built-in far-infrared sensors (Marif Co., Japan). Each camera was placed in a plastic bag and metal box to protect it from rain. We placed one camera per tree on a branch in the arboreal layer and aimed it at a wooden platform on which we placed a pile of fully ripe fruits from the same tree (Fig. 1). However, these fruit piles are viewed as unnatural by frugivores. Therefore platforms with fruits were set one week prior to the onset of the study to allow frugivores to become accustomed to their presence. The number of fruits in the piles varied according to the fruit size, ranging from five (*Artocarpus nobilis*, *Cullenia rosayroana*) to 50 (*Walsura trifoliata*). To record terrestrial frugivores we suspended cameras from a shrub, 1 m above a pile of fruits on the ground. These fruit piles were under the same fruiting trees that contained arboreal cameras and consisted of the same number of fruits of the same species. Most focal tree species had large crop sizes and ripe fruits were common on the ground, therefore we felt confident that our piles of fruit were not viewed as artificial by the terrestrial frugivores.

The built-in far-infrared sensor and the auto-quartz timepiece in each camera allowed us to document the time of each animal's visit. When an animal visited a pile of fruits, the sensor detected the far-infrared rays radiated from its body, and the camera was triggered. One photograph was taken every five seconds for as long as the animal was detected at the fruit pile by the camera's sensor.

Cameras were set in the morning (between 08:30h and 10:30h am) and checked every 3–4 days to minimize human disturbance. Data were collected continuously over two to three weeks per fruit species and at least 40 shots were taken per individual fruit tree. Because the duration of the experiment was different for the different fruiting species, we standardized visit frequency to number of visits per ten-day period.

RESULTS

The cameras yielded a total of 1795 photographs, of which 1628 (90%) showed an animal. We could identify 23 species from these photographs (Table 2). Because we could not consistently identify three spe-

FIG. 1. A platform with bait fruits in the arboreal layer. The camera was fixed to a branch.

TABLE 2. List of animal species captured by automatic cameras and number of visits (number of captures counted as number of visits). Bold letters indicate the nocturnal consumers, G indicates occurrence on the ground, A in the arboreal layer.

Group	Common name	Scientific name	Layer	Number of visits	Number of plants visited	Abbreviations
Rodentia	Murds	Three species	G + A	237	10	Murids
	Greater bandicoot rat	*Bandicota indica*	G	53	2	B. rat
	Jungle squirrel	*Funambulus layardi layardi*	G + A	254	10	J. squirrel
	Western giant squirrel	*Ratufa macroura melanochra*	A	47	3	G. squirrel
	Dwarf flying squirrel	*Petinomys fuscocapillus layardi*	A	143	2	F. squirrel
	Shrew		G	19	1	Shrew
Primates	Leaf monkey	*Trachypithecus vetulus*	A	176	6	L. monkey
	Slender Loris	*Loris tardigradus*	A	29	2	Loris
Chiroptera	Short-nosed Fruit bat	*Cynopterus sphinx*	A	65	2	Bat
Artiodactyla	Mouse deer	*Moschiola meminna*	G	134	7	M. deer
	Wild boar	*Sus scrofa cristatus*	G	19	1	Wild boar
Carnivora	Brown mongoose	*Herpestes fuscus rubidior*	G	18	1	B.mongoose
	Ring-tail civet	*Viverricula indica mayori*	G	107	4	R. civet
	Golden palm civet	*Paradoxurus zeylonensis*	G + A	30	3	G. civet
Aves	Sri Lanka myna	*Gracula ptilogenys*	A	120	2	Myna
	Sri Lanka orange-billed babbler	*Turdoides rufescens*	A	17	1	Babbler
	Ashy-headed laughine thrush	*Garrulax cinereifrons*	A	16	1	Thrush
	Bronze-winged pigeon	*Chalcophaps indica*	G	20	2	B. pigeon
	Sri Lanka grey hornbill	*Ocyceros gingalensis*	A + G	61	2	Hornbill
	Sri Lanka spurfowl	*Galloperdix bicalcarata*	G	27	2	S. fowl
	Sri Lanka junglefowl	*Gallus lafayetti lafayettii*	G	36	3	J. fowl
			Total	1628		

cies of small mice we treated them as a single group ("murids"). This yielded a total of 21 species for analysis. We were also unsuccessful in identifying one species of shrew. Of the 23 species, 14 were mammals: six Rodentia, three Carnivora, two primates, two Artiodactyla, and one Chiroptera. The remaining seven species were birds.

Animal assemblages differed between the arboreal and terrestrial layers (Figs. 2 and 3). The Sri Lanka grey hornbill (*Ocyceros gingalensis*), the flame-striped jungle squirrel (*Funambulus layardi layardi*), the murids, and the golden palm civet (*Paradoxurus zeylonensis*) were recorded visiting fruit piles both in the arboreal and on the terrestrial layers (Table 2). Most species, however, were recorded either in the arboreal or on the terrestrial layers. Both assemblages were taxonomically diverse, without any one taxon dominating. The diurnal and nocturnal assemblages were completely different and no species was found to be active during both day and night. In the diurnal assemblage, birds were the dominant (n = 7) component, while in the nocturnal assemblage it was mammals (n = 10).

Piles of most of the fruit species were visited on the arboreal and in the terrestrial layers (Fig. 4), except for *Podadenia thwaitesii* which was visited only in the arboreal layer. A higher number of animals visited piles on the terrestrial layer than in the arboreal layer (Fig. 4). Of these study fruits, 40 % of the fruiting species were visited by an equal number of animal species in both layers. *Cullenia ceylanica*, *Garcinia hermonii*, and *Walsura trifoliate* were not visited during the day time in the arboreal layer, while *P. thwaitesii*, *Glennia unijuga*, *Horsfieldia iriya*, and *Prunus walkeri* were not visited at night in the arboreal layer. These data demonstrate that the number and identity of foraging frugivores varies with time and forest layer.

Table 3 shows the frequency of frugivore visits to each fruit species. Mice and jungle squirrels visited ten fruiting species and therefore displayed a wider diet

than the other species we recorded, many of which were seen at only a few species of fruiting trees (Table 3). Birds were especially likely to be recorded at only one or two species of fruits, most commonly *Cullenia rosayroana*. Five species were visited by only two species of frugivore, always two mammals species.

We could identify 21 animal species during this study. Of these animals, 42% were entirely arboreal consumers while 37% were entirely terrestrial consumers. The remainder consumed fruits while moving between both layers. In addition, 48% of the animals were diurnal and the remainder nocturnal frugivores.

DISCUSSION

Since no detailed studies on fruit-frugivore relationships in Sri Lanka exist, this study provides some findings towards an understanding of the consumers of large-seeded fleshy fruits in the Sinharaja tropical rain forest. In our study we dealt with fifteen large-seeded fruits and a diverse assemblage of frugivores in a Sri Lankan forest, and registered visitors at the trees 24 hours a day, both in the arboreal and terrestrial layers.

Our results demonstrate that automatic cameras are important tools for recording animal activity at fruiting trees; they allowed us to detect frugivory by species that we would most likely have missed without them, especially shy nocturnal animals like slender loris (*Loris tardigradus*) and mouse deer (*Moschiola meminna*).

However, cameras in studies such as ours have potential limitations. The flash and the platforms could alter an animal's behavior, so to minimize this effect we placed platforms and cameras one week prior to the start of the study. Another limitation of automatic cameras is that they sometimes yielded pictures without an animal or with only part of a body in view.

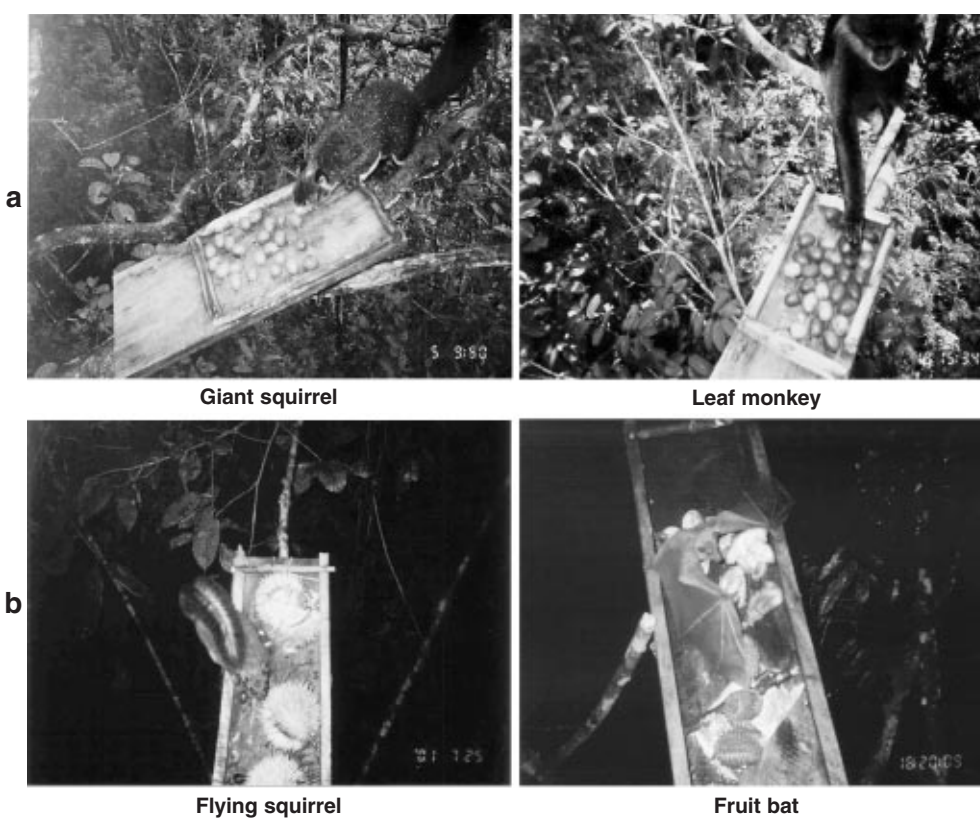

FIG. 2. Some of the arboreal-dwelling animals captured by the camera system (a) diurnal consumers, (b) nocturnal consumers.

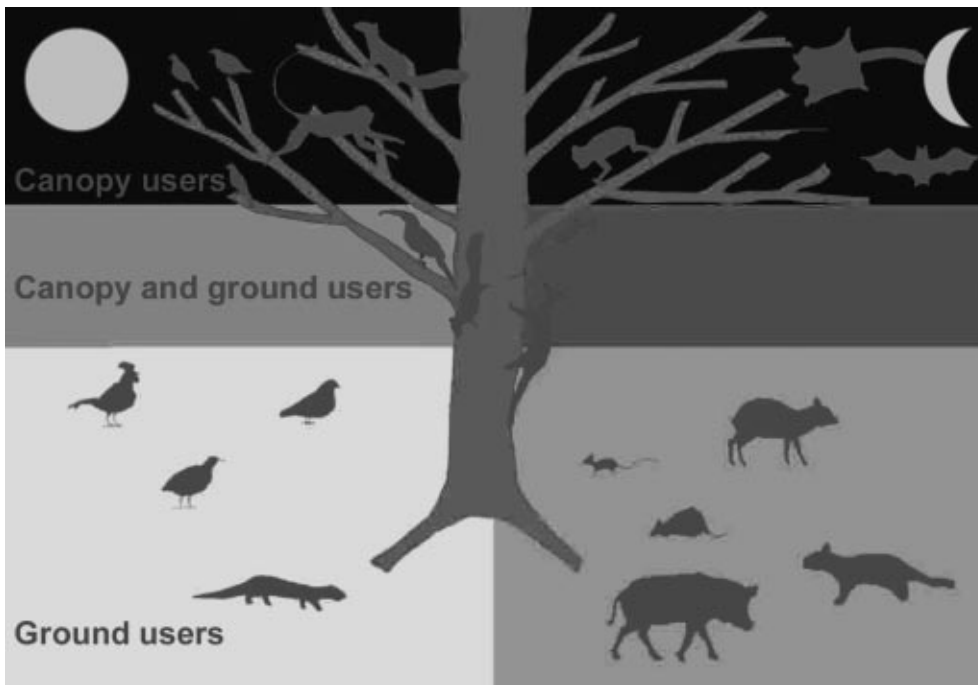

FIG. 3. Frugivore community recorded in the study and the utilization of layer and time.

We suspect this happened when animals passed the camera quickly and the camera was triggered too slowly. Cameras with adjustable sensors would, most likely, eliminate this problem. On the other hand, animals that remain too long in front of the camera use up much film material, hence later visitors might go unrecorded. To avoid this error it is necessary to repeat camera trappings. Yet another limitation of cameras is that they only record directly in front of the lens the animals that visited the fruit piles. Further, there is a possibility that some animals do not visit fruit piles but do consume fruits at the tree. It is possible to improve this by setting the cameras very close to the fruits in branches. However, this will be practically difficult because most fruits are found at the margins and at the tips of branches. So it is very difficult to set the cameras accordingly. Placement of cameras on the terrestrial layer is also an important consideration. If a camera is close to a target of fruit, it works well for small animals (e.g., murid rodents) but not for the larger ones. If, on the other hand, the camera is placed relatively far from fruit piles the situation is reversed, which was a problem in our study. We recommend carrying out a preliminary study to determine which animals visit and the best distance from fruits to place the cameras. As a result of all these limitations we understand that in order to get a complete picture of the frugivore assemblage it is not sensible to depend on the camera trappings alone, but that it is necessary to combine direct observation with camera trappings.

We recorded only 23 different animal species at fruiting trees. This figure did not include small species of frugivorous birds such as bulbuls, white-eyes, and babblers, and because we focused on large-fruited species we were unlikely to detect such birds. Another factor is that the Sinharaja forest has a low diversity of large frugivorous mammals and birds. For example, only two species of monkey are present: the western purple-faced leaf monkey (*Trachypithecus vetulus*) and the western toque macaque (*Macaca sinica aurifrons*) (Kotagama & Karunarathna 1983). Macaques are rare in the interior of the forest, but abundant at its periphery. During this study they were not recorded. Likewise, we did not record any large fruit bats inside the forest; they too are typically at the

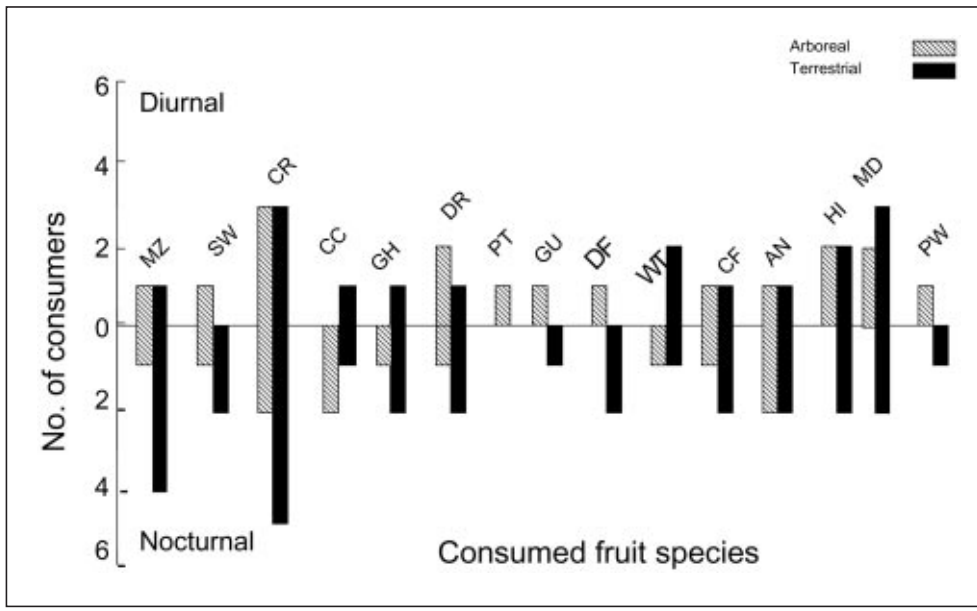

FIG. 4. Number of consumers of the different fruit species at the different layers in the 24- hour cycle (for abbreviations of plant species see Table 1).

TABLE 3. Frequency of visit by different consumers for different fruit species. Bold letters indicate nocturnal consumers (for abbreviations of animal species see Table 2).

Animals	MZ	SW	CR	CC	GH	DR	PT	GU	DF	WT	CF	AN	HI	MD	PW
Mice	1.6	–	2.3	1.9	3.1	2.2	1.8	–	–	1.9	2.1	–	–	5	1.8
B. rat	–	–	2.1	–	–	–	–	–	–	–	–	3.2	–	–	–
J. squirrel	9.2	1.9	2.7	1.3	1.4	2.6	–	–	–	1.8	1.7	–	1.5	1.3	–
G. squirrel	–	–	–	0.8	–	–	–	–	–	–	2.5	1.4	–	–	–
F. squirrel	–	7.3	7	–	–	–	–	–	–	–	–	–	–	–	–
Shrew	1.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–
L. monkey	–	–	2.3	–	–	2.4	2.8	2.4	5.6	–	–	–	–	–	2.1
Loris	–	–	1.5	–	–	–	–	–	–	–	–	1.4	–	–	–
Bat	–	–	–	3.3	–	3.2	–	–	–	–	–	–	–	–	–
M. deer	2.4	–	1.8	–	–	1.8	–	1.6	2.6	–	1.7	–	1.5	–	–
Wild boar	1.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–
B. Mongoose	–	–	–	–	–	–	–	–	–	–	–	–	–	1.8	–
R. civet	–	–	2.3	–	1.9	–	–	–	–	–	–	4.8	–	1.7	–
G. Civet	1	–	0.9	–	–	–	–	–	–	–	–	1.1	–	–	–
Myna	–	–	–	–	–	–	–	–	–	–	–	–	6	6	–
Babbler	–	–	1.7	–	–	–	–	–	–	–	–	–	–	–	–
Trush	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–
B. pigeon	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
Hornbill	–	–	–	–	–	–	–	–	–	–	–	–	1.1	5	–
S. fowl	–	–	0.9	–	–	–	–	–	–	1.8	–	–	–	–	–
J. fowl	–	–	–	–	–	–	–	–	–	1	–	1.2	1.4	–	–

periphery of the forest (de Zoysa & Raheem 1987). Among the birds, only three large species are found in Sinharaja: one species of hornbill (*Ocyceros gingalensis*) and two pigeons (*Ducula aenea* and *Columba torringtoni*). We detected neither species of pigeon. We recorded only seven bird species, six of which are endemic to Sri Lanka (Kotagama & Fernando 1994).

We found that frugivore assemblages differed between arboreal and terrestrial layers and between diurnal and nocturnal periods. Birds were the dominant component of the diurnal assemblage. Among the bird species we observed, only the Sri Lanka grey hornbill, the Sri Lanka myna (*Gracula ptilogenys*) and bronze-winged pigeon (*Chalcophaps indica*) were obligate frugivores, likely to disperse the large seeds of the plant species we studied (Legge 1983). Mammals dominated the nocturnal assemblage and have the ability to disperse large seeds. Finally, there was little difference in body size and likely dispersal ability between arboreal and terrestrial frugivores; at both levels large animals were common consumers of fruits.

Harrison (1962), Charles-Dominique (1975), Whitmore (1975), Gautier-Hion (1985), Van Schaik & Griffiths (1996) and Miura *et al*. (1997) reported that many animals move between forest layers. We found four species that did so. One, the Sri Lanka grey hornbill, is generally arboreal, but moved frequently between ground and canopy to consume fruits of two trees, *Horsfieldia iriya* and *Myristica dactyloides*. These were the only two species of fruit we observed that hornbills consumed and they may have been highly preferred species. We know that these two species have a high concentration of lipids and energy (Jayasekara, unpublished) and it is known that hornbills prefer lipid-rich fruits in Bornean forest (Leighton 1986). We know of no previous study reporting terrestrial foraging by arboreal hornbills.

The fact that no animal species at our site was active both day and night, this means that if we had relied on observations solely during the day or night, we would have failed to observe an important part of the frugivore assemblage. For example, mouse deer (*Tragulus javanicus*) and wild boar (*Sus scrofa*) were found active irrespective of time of day in Indonesia and Malaysia (Van Schaik and Griffiths 1996, Miura *et al*. 1997). The same species of boar and a closely related species of mouse deer occur at our Sri Lankan site and were active only at night. We suspect this geographic difference in activity cycles is related to differences in food availability. However we recorded wild boar only 19 times and this may be not enough to determine a wild boar activity pattern.

The present study confirms that a considerable number of species of frugivores consumed large fleshy fruits in the Sinharaja rain forest on the ground and in trees and in a 24-hour period. However, it is not advisiable to rely entirely either on automatic cameras or on direct observation to gain a complete picture of frugivore assemblage, because both methods have limitations. Therefore in order to obtain a complete picture of a frugivore assemblage it is necessary to employ both methods in tandem.

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