Ecol Res (2010) 25: 225–231
DOI 10.1007/s11284-009-0650-1

ORIGINAL ARTICLE

Soumya Prasad · André Pittet · R. Sukumar

Who really ate the fruit? A novel approach to camera trapping for quantifying frugivory by ruminants

Received: 2 March 2009 / Accepted: 28 August 2009 / Published online: 16 October 2009
© The Ecological Society of Japan 2009

Abstract Tropical forest ruminants disperse several plants; yet, their effectiveness as seed dispersers is not systematically quantified. Information on frequency and extent of frugivory by ruminants is lacking. Techniques such as tree watches or fruit traps adapted from avian frugivore studies are not suitable to study terrestrial frugivores, and conventional camera traps provide little quantitative information. We used a novel time-delay camera-trap technique to assess the effectiveness of ruminants as seed dispersers for *Phyllanthus emblica* at Mudumalai, southern India. After being triggered by animal movement, cameras were programmed to take pictures every 2 min for the next 6 min, yielding a sequence of four pictures. Actual frugivores were differentiated from mere visitors, who did not consume fruit, by comparing the number of fruit remaining across the time-delay photograph sequence. During a 2-year study using this technique, we found that six terrestrial mammals consumed fallen *P. emblica* fruit. Additionally, seven mammals and one bird species visited fruiting trees but did not consume fallen fruit. Two ruminants, the Indian chevrotain *Moschiola indica* and chital *Axis axis*, were *P. emblica*'s most frequent frugivores and they accounted for over 95% of fruit removal, while murid rodents accounted for less than 1%. Plants like *P. emblica* that are dispersed mainly by large mammalian frugivores are likely to have limited ability to migrate across fragmented landscapes in response to rapidly changing climates. We hope that more quantitative information on ruminant frugivory will become available with a wider application of our time-delay camera-trap technique.

Keywords Deer · Mudumalai · *Phyllanthus emblica* · Seed dispersal · Ungulates

Introduction

Southeast Asian large mammal declines are among the most serious global extinction crisis (Corlett 2007; Sodhi et al. 2004). The Indian subcontinent is the last refuge for Asian ruminants whose range extends as far west as India, such as the hog deer and the gaur (Simon Stuart, pers. comm.; Duckworth et al. 2008; Timmins et al. 2008). Tropical Asian ruminants have mostly been researched as food for carnivores (Karanth et al. 2004) and there is little information available on the other ecological roles of these fascinating animals. In particular, their role in seed dispersal is poorly understood, though they are known to disperse several large (>1 mm) as well as small-seeded species. (Chen et al. 2001; Middleton and Mason 1992; Prasad et al. 2006). Given their large home ranges and long seed retention times, ruminants are potential long-range dispersers for several tropical plants (Cosyns et al. 2005; Mouissie et al. 2005; Vellend et al. 2003). Yet, the effectiveness of ruminants as seed dispersers is poorly understood.

Disperser effectiveness is defined as the contribution a disperser makes to the future reproduction of a plant. Information required to evaluate disperser effectiveness falls into three broad categories: (a) the quantity of fruit removed, (b) the quality of fruit handling and seed deposition, and (c) the diversity of species dispersed (taxonomic and seed size range) (Dennis and Westcott 2007; Schupp 1993). While the qualitative aspects of seed dispersal by ruminants have been addressed to some extent (Cosyns et al. 2005; Mouissie et al. 2005;

Electronic supplementary material The online version of this article (doi:10.1007/s11284-009-0650-1) contains supplementary material, which is available to authorized users.

S. Prasad (✉) · R. Sukumar
Centre for Ecological Sciences,
Indian Institute of Science, Bangalore 560012, India
E-mail: prasadsoumya@gmail.com
Tel.: +91-9448542902
Fax: +91-80-23602280

A. Pittet
Centre for Electronic Design and Technology,
Indian Institute of Science, Bangalore 560012, India

Prasad et al. 2006), little is known about the quantity or diversity of dispersal services provided by ruminants. The quantity of seed dispersal depends on the number of visits made to the plant by a disperser and the number of seeds removed per visit (Schupp 1993).

Understanding quantitative aspects of frugivory by terrestrial animals such as ruminants is limited by methodological constraints since most available techniques, such as tree watches or fruit traps, have evolved from studies of arboreal frugivores (such as birds, bats, or primates) and are not suitable for studying terrestrial frugivores. Tree watches require one or two observers to watch fruiting trees to note whether the visiting animals consume fruit, the number of fruit they consume, and their fruit handling behavior (for e.g., Dennis and Westcott 2006). Large terrestrial frugivores such as ruminants or pheasants are often nocturnal or are extremely wary of human presence and this makes it difficult to observe them directly by watching fruiting trees. Fruit fall traps are placed beneath and around fruiting trees to note fruit-fall rates and the proportion of fruit-bearing feeding signs, from which proportion of fruit removed by frugivores is deduced using various approaches (for e.g., Howe 1980). Placing fruit traps obstructs movement and frugivory by terrestrial frugivores and is hence not suitable to quantify frugivory by ruminants.

Camera traps are indeed a useful technique for studying terrestrial frugivores and have been used extensively for this purpose (for e.g., Babweteera et al. 2007; Beck and Terborgh 2002; Christianini and Galetti 2007; Cramer et al. 2007; Jayasekara et al. 2003; Kitamura et al. 2007; Miura et al. 1997). These previous studies have used camera traps to identify potential terrestrial frugivores, but they fail to distinguish frugivores from mere visitors to fruiting trees. This is because they do not set clear criteria to distinguish confirmed frugivory events (when fruit were actually consumed by an animal) to situations involving animals that were simply walking past the fruiting tree without consuming fruit. In the absence of this distinction being made about identifying actual frugivores using camera traps, the study of terrestrial frugivores has been data-deficient compared to research on arboreal frugivores. We attempted to develop a technique by which we could obtain confirmed frugivory events using a camera trap in order to distinguish frugivores from visitors as well as obtain data on the quantity of fruit consumed per visit by a frugivore.

In this paper, we illustrate the use of this novel camera-trapping technique to address the quantitative aspects of dispersal services provided by ruminants using the example of *Phyllanthus emblica* (Euphorbiaceae, Gærtn), whose fruit are important non-timber forest produce from Asian dry tropics. Our main objectives were to: (1) distinguish visitors from consumers of fallen *P. emblica* fruit using camera traps; (2) quantify and compare fruit removal by ruminants with other terrestrial frugivores of *P. emblica*.

Materials and methods

Study area and study species

Mudumalai (321 km^2; 11°32′–11°43′N, 76°22′–76°45′E) is part of a large, contiguous dry forest track in southern India. These forests have a diverse and abundant ruminant assemblage consisting of species such as gaur *Bos gaurus*, sambar *Cervus unicolor*, chital *Axis axis,* barking deer *Muntiacus muntjak*, and Indian chevrotain *Moschiola indica* (Varman and Sukumar 1995). This study was carried out at the 50-ha Mudumalai forest dynamics plot (MFDP), where the woody plant community composition, recruitment, and mortality patterns have been monitored since 1988 (Sukumar et al. 1992). The MFDP received 1200 ± 103 mm of rainfall annually in the last decade.

The study tree, *P. emblica* bears globose, greenish, drupaceous fruit (length 20–30 mm) from October to February. These fruit are extensively harvested by people across its range in Asian tropics for use in food products and cosmetics. Previous work using tree watches has shown that *P. emblica*'s arboreal frugivores are either largely seed predators (giant squirrel *Ratufa indica*) or mainly pulp-feeders (Hanuman langur *Semnopithecus entellus*) that were neutral with respect to dispersal action (since langur drop fruit and seed under parent plants). However, langur facilitate frugivory by terrestrial animals like ruminants, by making large quantities of fruit available to them on the ground. The terrestrial frugivores, ruminants, and murid rodents, remove seeds from the vicinity of the parent plants (Prasad et al. 2004). The role of rodents in this system is poorly understood; they are known to predate seeds but not scatter hoard them. Earlier work on the qualitative aspects of ruminant frugivory, using gut passage trials and germination experiments, has shown that ruminants swallow fruit whole and disperse viable *P. emblica's* seeds through regurgitation after retaining them in the rumen for several hours (Prasad et al. 2006). Tree watches used in the earlier study provided a list of frugivores and their fruit-handling behavior, but the quantity of fruit consumed by different frugivores could not be inferred by this technique (Prasad et al. 2004). This was because observers had to be located over 100 m from trees since large mammalian frugivores were wary of human presence. From these distances it was difficult to confirm frugivory or note number of fruit removed. Thus the quantity of *P. emblica* fruit removed by different ruminant species and murid rodents remains to be addressed.

Methods

On the MFDP, we monitored frugivory of *P. emblica* using four camera traps for two consecutive fruiting seasons (15 trees in 2005–2006; 19 trees in 2006–2007).

These focal trees were monitored for crop size, neighborhood densities, and fruit removal as part of a larger study examining factors influencing fruit removal. To study frugivory, we used digital camera traps (PIRPIC04) developed by one of us (A. Pittet) at the Centre for Electronics Design and Technology (CEDT), Indian Institute of Science, Bangalore. These systems use passive infrared motion sensors to detect the movement of any warm-bodied animal passing in front of them. The sensor is connected to a micro-controller that, in turn, can trigger the digital camera (Olympus D-380 or C-120, 2 megapixels) when required. The batteries used last for at least 5 days, always ready to take a picture within less than a second. The motion detector has adjustable sensitivity and is able to detect even small rodents or birds at more than 8–10 m. However, at night, the effectiveness of the flash is a limiting factor as the clarity of the picture is reduced significantly beyond 6 m. The camera, sensor, and the micro-controller were together housed in weatherproof casing and left on continuously throughout the day and night (for more details on PIRPIC04 refer Varma et al. 2006).

The principal difference from camera traps used before in frugivory studies was that our units were reprogrammed to take time-delay pictures every 2 min, for the next 6 min after it was first triggered, yielding a sequence of four pictures (0, 2, 4, and 6 min). By comparing the number of fruit seen in earlier pictures with later pictures in this sequence, we could infer whether an animal that visited the tree had consumed fruit (for examples see Fig. 1; Figs. S.1, S.2). When animals stayed beyond 6 min, the camera was triggered again. The time-delay sequence helped us distinguish actual frugivores from mere visitors. This technique also yielded information on the number of available fruit consumed by a frugivore as well as the length of time frugivores spent at fruiting trees.

The camera-trap unit was secured to the trunk of a focal tree and kept focused on fallen fruit beneath the tree. Only fallen fruit were considered for camera trapping; fruit were never interchanged between trees, though fruit from the same tree were often moved from their original locations to be placed in front of the camera. The camera traps were checked daily, they were never set for more than two consecutive days at a tree and each focal tree was sampled for a minimum of 100 h (4 days). Each day we noted the number of pictures taken, fruit remaining from the previous day, and fruit placed in the front of the camera that day. Photographs were transferred to a computer and examined closely to check if fruit had been consumed using the time-delay sequence. All analyses and graphs were processed in the open-source software R 2.8.0. Results are presented as mean ± SE.

Data collection began only after an initial trial period to fine tune camera placement (~20 days), due to which fewer days were sampled in the first year. To check if camera placement disrupted frugivore activity, we monitored fruit removal in the fruit-fall region away from the camera trap (cameras covered only a part of the fruit-fall area) and in adjacent fruiting trees. When fruit placed in front of the camera remained while they were removed from elsewhere, it implied that our camera placement had disturbed frugivores. After such trials, camera placement was standardized to a height of 1.3–1.7 m, which appeared not to disrupt frugivore

Fig. 1 Camera-trap pictures of a frugivore (Chital *Axis axis*) consuming fallen fruit at a *Phyllanthus emblica* tree. After being triggered by animal movement, the camera was programmed to take a picture at intervals of 2 min for the next 6 min, yielding a sequence of four pictures (**a** 0, **b** 2nd, **c** 4th, **d** 6th min). Examining the difference in number of fruit seen in this time-delay sequence of pictures reveals that the chital consumed the four fallen fruit set in front of the camera within 2 min

activity probably because it kept cameras above the eye of frequent terrestrial frugivores (but within range of our flash). Camera units were camouflaged by painting them green and by covering them with foliage and elephant dung (to mask human odor). We also attempted to quantify the bias due to flash activity at night by placing an infrared video camera trap (Sony CCD TR511E) along with our regular camera-trap units. The video camera was also kept focused on fallen fruit and was triggered by a mechanism similar to PIRPIC04. However, due to several technical problems with our sole video camera we managed to video tape only two flash-events involving *P. emblica's* most frequent nocturnal frugivore (i.e., the Indian chevrotain). It appeared that this frugivore was not affected by the flash. Videos shot in infrared (which is not visible to most vertebrates) showed that the chevrotain did not move away after the flash and continued to feed on fruit as before.

Results

The camera traps sampled a total of 3120 hours or 130 days across 2 years and over 30 fruiting *P. emblica* trees for terrestrial frugivore activity. Species that were noted to remove fallen *P. emblica* fruit by comparing pictures in the time-delay sequence generated by our camera trap unit were classified as frugivores, while others were noted as visitors. In this fashion, we classified six mammals as frugivores of *P. emblica*; this included three ruminants (chital, Indian chevrotain, and barking deer), a rodent (black rat *Rattus rattus)*, a primate (langur) and the elephant *Elephas maximus* (Table 1). Of these, the langur is a frequent arboreal frugivore (Prasad et al. 2004) which consumed fallen fruit on one occasion across 2 years. Seven mammal species and one bird species were noted to visit fruiting *P. emblica* trees but not consume any available fallen fruit. The sole avian visitor was the Magpie robin *Copsychus saularis* (year 1 = 1, and year 2 = 0 visits). The mammalian visitors included a ruminant (sambar, year 1 = 1, year 2 = 2 visits), a primate (bonnet macaque *Macaca radiata*, year 1 = 0; year 2 = 1 visits), a rodent (white-tailed wood rat *Madromys blanfordi,* year 1 = 1; year 2 = 2 visits), the sloth bear *Melursus ursinus* (year 1 = 0; year 2 = 1 visits), two species of mongoose (stripe-necked mongoose *Herpestes vitticollis,* year 1 = 0; year 2 = 1 visits; ruddy mongoose *Herpestes smithii*, year 1 = 2; year 2 = 0 visits) and the leopard (*Panthera pardus,* year 1 = 0; year 2 = 1 visits). These visitor species were never observed to consume fruit by camera traps, direct observations or other methods outlined in Prasad et al. (2004). On two occasions in both years, we obtained pictures of animals (small rodents or what appeared to be a shrew) that could not be clearly identified and none of these unidentified animals consumed fruit.

Frequency of visits

On average, there were 0.71 ± 0.09 (max = 5, *n* = 130 days) visits per day to fruiting *P. emblica* trees by its frugivorous species, while the visitor species were less frequent (0.12 ± 0.03 visits per day). Frugivory by the Indian chevrotain and chital, the two most frequent frugivores, was noted within the first 12 days of camera-trap sampling and no new frugivore species were detected beyond 47 days of sampling. Thus, the second year of camera-trap sampling (75 days) did not detect any new frugivore species for *P. emblica.*

Ruminants were the most frequent terrestrial frugivores of *P. emblica*. The Indian chevrotain was the most frequent frugivore species in the first year though chital was more frequent in the second year. These two ruminant species together constituted 84% (*n* = 90) of frugivore visits to fruiting *P. emblica* trees. Among the other ruminant species that visited fruiting *P. emblica* trees, barking deer ate *P. emblica* fruit on rare visits (Table 1), while sambar was never observed to consume *P. emblica* fruit. The non-ruminant frugivores, which included langur, elephant, and the black rat, were noted to remove fallen *P. emblica* fruit on one occasion each during the 2 years of sampling (Table 1). Even the frequent frugivore species did not consume available fallen fruit on every visit (Table 1), and this was especially true

Table 1 Frequency of visits and quantity of fruit removed by different frugivores of *Phyllanthus emblica* as observed by camera traps (year 1 15 trees, 54 days; year 2 19 trees, 76 days)

Frugivore	Frequency of visits		Average proportion of fruit consumed per visit		Relative fruit removal		Average visit length (min)	
	Year 1	Year 2	Year 1 (%)	Year 2 (%)	Year 1 (%)	Year 2 (%)	Year 1	Year 2
Chital	14 (11)	19 (14)	70 ± 11	72 ± 10	29 (86/300)	53 (66/125)	4.6 ± 1.3	3.8 ± 0.9
Indian chevrotain	33 (27)	10 (10)	80 ± 6	65 ± 13	66 (197/300)	47 (59/125)	4.8 ± 0.7	3.6 ± 0.5
Black rat	9 (1)	–	1 ± 1	–	0.3 (1/300)	–	2.7 ± 0.7	–
Langur	1 (1)	1 (0)	40	0	1 (4/300)	0 (0)	5	2
Barking deer	1 (1)	–	33	–	1 (2/300)	–	2	–
Elephant	1 (1)	–	100	–	3 (10/300)	–	2	–

Results are mean ± SE. Relative fruit removal is the ratio of number of fruit removed by a frugivore across the entire fruiting season to the total number of *P. emblica* fruit consumed by all frugivores. *Figures in parentheses* for the 'frequency of visits' column represent the number of visits where fruit were actually removed by a frugivore for the black rat, which removed fruit only once across nine visits.

Proportion of fruit removed by different frugivores

On average, the Indian chevrotain and chital consumed around 70% of the available fallen fruit per visit. On one occasion across 2 years, barking deer, langur, and elephants consumed considerable proportions of available fallen fruit (33, 40, and 100%, respectively). Over 95% of the total *P. emblica* fruit removed by frugivores and having the potential to be dispersed were consumed by ruminants (year 1, 285 of 300 fruit; year 2, 125 of 125 fruit removed by frugivores). There was a shift in the relative proportion of fruit removed by the chevrotain and chital from the first to the second year. The relative proportion of fruit removed by the chevrotain ($\sum$ fruit removed by chevrotain/$\sum$ fruit removed by all frugivores) declined by 19% (Table 1; χ^2 test with continuity correction, $\chi^2 = 11.80$, P-value <0.001) while the relative proportion of fruit removed by chital increased by 24% in the second year ($\chi^2 = 21.33$, P-value <0.001).

Frugivore visitation pattern

Chital visits to fruiting *P. emblica* trees were largely diurnal, peaking in the early morning and evening hours, with a few rare visits during night hours (Fig. 2). In contrast, the chevrotain frequented fruiting *P. emblica* trees only during the night hours, with most of the visits occurring between 1900 and 1400 hours. The black rat too was nocturnal, with visits spread between 1900 and 0600 hours. Visits by other frugivore species that consumed fallen *P. emblica* were too infrequent to characterize visitation patterns. The duration of visit to fruiting *P. emblica* trees as noted by the camera trap (obtained by the number of times an animal appeared in the time-delay sequence) was similar in the 2 years for the three frequent frugivores (Table 1). Chital spent generally between 2 and 8 min per visit searching for *P. emblica* fruit. On one rare occasion, chital were noted to spend up to 52 min (year 1) when they were following langur foraging activity at fruiting *P. emblica.*

Discussion

From two fruiting seasons and over 3000 hours of camera-trap observations using the time-delay technique, for the first time we report quantitative information on frugivory by terrestrial animals. With our time-delay camera-trap technique we could obtain pictures that differentiated events when fallen fruit were actually removed by frugivores compared to mere visits. The time-delay camera-trap technique showed that ruminants were the most frequent terrestrial frugivores of *P. emblica* and that they accounted for over 95% of the fallen fruit removed by frugivores. From earlier studies, it is known that *P. emblica's* arboreal frugivores are largely neutral or predatory in dispersal action, while ruminants disperse viable seeds through regurgitation (Prasad et al. 2004, 2006). Thus, based on results from our camera-trap work, we can now say that ruminants remove the largest proportion of *P. emblica's* fruit and are *P. emblica's* principal primary disperser.

In the second year, a higher proportion of fruit was removed by chital compared to the first year where chevrotain removed more fruit. Though we sampled more days in the second year, there were fewer species recorded to consume fallen *P. emblica* fruit. The fruiting scenario on the MFDP differed between the two study years with the estimated quantity of *P. emblica* fruit available to frugivores being 73% higher in the first year(∼260,000 fruit) compared to the second (∼150,000 fruit) (Prasad, unpublished data). Given that chital is a larger animal (40–100 kg) compared to the Indian chevrotain (2–4 kg, Menon 2002), it is possible that it is a superior competitor when resources are scarce, as during the second *P. emblica* fruiting season. It is also possible that the chevrotain visits declined in the second year since it was not worthwhile for smaller animals like them to expend effort in searching when very few fallen fruit were available. Shifts in resource usage due to possible competitive exclusion when resources are lim-

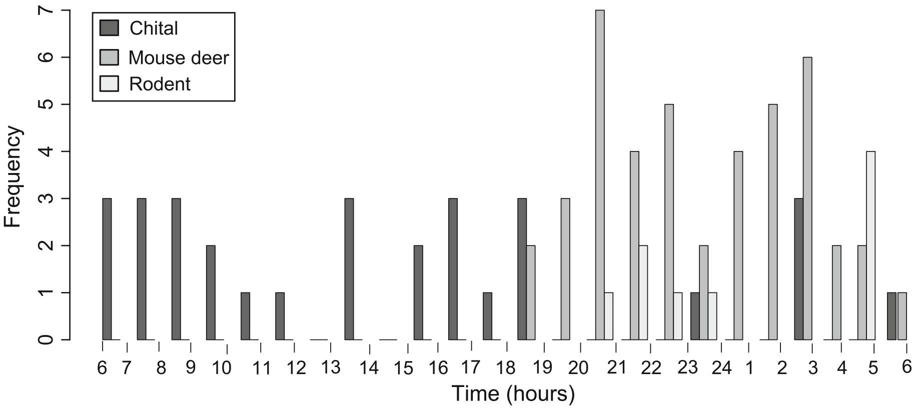

Fig. 2 Activity patterns of the three frequent frugivore species of *Phyllanthus emblica* at fruiting trees. Chital deer *Axis axis* frequented fruiting *P. emblica* trees largely in the daytime (0600–1800 hours), while the Indian chevrotain *Moschiola indica* and the rodent, Black rat *Rattus rattus*, visited the fruiting tree only at night (1800–0600 hours)

iting has been documented for other ruminant species (Bagchi et al. 2004; Gordon and Illius 1989; Stewart et al. 2002). The higher diversity of frugivore assemblage in the first year could also possibly be due to the super abundant fruit attracting several animals that might otherwise rarely consume these fruit (such as barking deer and the elephant).

Through camera trapping, three species were added to the previously known list of *P. emblica's* frugivores that was obtained from direct observations of fruiting trees (Prasad et al. 2004). This included the Indian chevrotain, the elephant, and the black rat. While the elephant and the black rat were noted to remove *P. emblica* fruit only on one rare occasion each, the chevrotain was a very frequent frugivore. Chevrotain visits to fruiting *P. emblica* trees were only at night (though it was photographed at other locations during the daytime in our study site), and it was a cryptic animal that kept to the under-growth and was never observed directly to consume *P. emblica* fruit (Prasad, pers. obs.). Camera trapping is a useful technique for studying such nocturnal or hard-to-observe frugivores. As shown by our data, terrestrial frugivores visited fruiting *P. emblica* trees once or twice per day. Using tree watches to study frugivory for species that are primarily dispersed by frugivores which visit fruiting trees infrequently yields very little data (for e.g., Babweteera et al. 2007; Prasad et al. 2004). Indeed, camera trapping is a more efficient method for obtaining information on such infrequent frugivory events. Further, large mammals like ruminants are extremely wary of any signs of human presence and our presence close to fruiting trees could deter them from approaching trees. As pointed out by Obrien and Kinnaird (2008) since camera traps sit unobtrusively in the forest, they are well suited to study animals that avoid humans or ones that might be influenced by the presence of an observer.

We would also like to highlight that not all vertebrate species that were photographed at fruiting *P. emblica* trees consumed its fruit. It is very important to make this distinction about confirming frugivory events, or else our study too would have noted many more than six terrestrial frugivores for *P. emblica* as reported by earlier studies (for e.g., Babweteera et al. 2007; Beck and Terborgh 2002; Christianini and Galetti 2007; Cramer et al. 2007; Jayasekara et al. 2003; Kitamura et al. 2007; Miura et al. 1997). It is also possible to make this distinction about confirming actual frugivory events using video camera traps. However, the available video camera traps are several times more expensive than photographic cameras, and they also have additional problems with image resolution and power requirements (especially for nocturnal events requiring supplementary lighting) that inhibit their implementation at larger scales (A. Pittet, pers. obs.). Hopefully, these technical problems with video camera traps will be resolved as both video and battery technology continues to improve. We would also like to add that while this study was being implemented digital camera traps having infra-red flashes have become more common and affordable, and offer promising solutions to possible flash-avoidance behavior of study animals (A. Pittet, pers. obs.).

Species like *P. emblica* that are mainly dependent on large-bodied, terrestrial mammalian frugivores like ruminants for dispersal are likely to be limited in their ability to migrate to more suitable locations in response to changing climates across fragmented landscapes compared to bird-dispersed or wind-dispersed species (Corlett 2009). In dry tropical forest sites like ours, up to 18% of the species are dispersed by ruminants (Prasad, unpublished data). It is important to understand the quantitative role of ruminants in the dispersal of others fruit species that they consume in order to identify plant species that might need our assistance to move across fragmented landscapes in response to changing climates. We hope that more quantitative information on frugivory by ruminants will become available with a wider application of our simple modification of the camera-trap technique.

Acknowledgments We wish to thank the Tamil Nadu forest department for providing permissions to carry out this work at Mudumalai, the Ministry of Environments and Forests for funds, and the camera-trap development team at the Centre for Electronic Design and Technology, Indian Institute of Science, for providing us the camera traps. The implementation of the camera trap technique in the field rested on the experience and knowledge of our field assistants, especially, Dhumba, Bomma, and Krishna. Special thanks to Karpagam Chelliah, Smita Nair, R.P. Harisha, Nisarg Prakash, and Raman Kumar for support at various stages of this work and to Kartik Shanker and Meena Venkatraman who helped identify the rodents.

References

Babweteera F, Savill P, Brown N (2007) *Balanites wilsoniana*: regeneration with and without elephants. Biol Conserv 134:40–47

Bagchi S, Mishra C, Bhatnagar YV (2004) Conflicts between traditional pastoralism and conservation of Himalayan ibex (*Capra sibirica*) in the trans-Himalayan mountains. Anim Conserv 7:121–128

Beck H, Terborgh J (2002) Groves versus isolates: how spatial aggregation of *Astrocaryum murumuru* palms affects seed removal. J Trop Ecol 18:275–288

Chen J, Deng XB, Bai ZL, Yang Q, Chen GQ, Liu Y, Liu ZQ (2001) Fruit characteristics and *Muntiacus muntjac vaginalis* (muntjac) visits to individual plants of *Choerospondias axillaris*. Biotropica 33:718–722

Christianini AV, Galetti M (2007) Spatial variation in post-dispersal seed removal in an Atlantic forest: effects of habitat, location and guilds of seed predators. Acta Oecol 32:328–336

Corlett RT (2007) The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica 39:292–303

Corlett RT (2009) Seed dispersal distances and plant migration potential in tropical East Asia. Biotropica 41:592–598

Cosyns E, Delporte A, Lens L, Hoffmann M (2005) Germination success of temperate grassland species after passage through ungulate and rabbit guts. J Ecol 93:353–361

Cramer JM, Mesquita RCG, Bentos TV, Moser B, Williamson GB (2007) Forest fragmentation reduces seed dispersal of *Duckeodendron cestroides*, a central Amazon endemic. Biotropica 39:709–718

Dennis AJ, Westcott DA (2006) Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. Oecologia 149:620–634

Dennis AJ, Westcott DA (2007) Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. Oecologia 149:620–634

Duckworth JW, Steinmetz R, Timmins RJ, Pattanavibool A, Zaw T, Tuoc D, Hedges S (2008) *Bos gaurus*. In: IUCN 2008. 2008 IUCN red list of threatened species. Available at http://www.iucnredlist.org

Gordon IJ, Illius AW (1989) Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79:383–389

Howe HF (1980) Monkey dispersal and waste of a neotropical fruit. Ecology 61:944–959

Jayasekara P, Takatsuki S, Weerasinghe UR, Wijesundara S (2003) Arboreal visitors in a tropical forest in Sri Lanka. Mamm Study 28:161–165

Karanth KU, Nichols JD, Kumar NS, Link WA, Hines JE (2004) Tigers and their prey: predicting carnivore densities from prey abundance. Proc Natl Acad Sci USA 101:4854–4858

Kitamura S, Suzuki S, Yumoto T, Poonswad P, Chuailua P, Plongmai K, Maruhashi T, Noma N, Suckasam C (2007) Dispersal of *Canarium euphyllum* (Burseraceae), a large-seeded tree species, in a moist evergreen forest in Thailand. J Trop Ecol 22:137–146

Menon V (2002) A field guide to Indian mammals. Dorling Kindersley, New Delhi

Middleton B, Mason DH (1992) Seed herbivory by Nilgai, Feral Cattle, and Wild Boar in the Keoladeo National Park, India. Biotropica 24:538–543

Miura S, Yasuda M, Ratnam LC (1997) Who steals the fruits? Monitoring frugivory of mammals in a tropical rain forest. Malay Nat J 50:183–193

Mouissie AM, van der Veen CEJ, Veen GF, van Diggelen R (2005) Ecological correlates of seed survival after ingestion by Fallow Deer. Funct Ecol 19:284–290

Obrien T, Kinnaird MF (2008) A picture is worth a thousand words: the application of camera trapping to the study of birds. Bird Conserv Int 18:S144–S162

Prasad S, Chellam R, Krishnaswamy J, Goyal SP (2004) Frugivory of *Phyllanthus emblica* at Rajaji National Park, north-west India. Curr Sci 87:1188–1190

Prasad S, Krishnaswamy J, Chellam R, Goyal SP (2006) Ruminant-mediated seed dispersal of an economically valuable tree in Indian dry forests. Biotropica 38:679–682

Schupp EW (1993) Quantity, quality, and the effectiveness of seed dispersal by animals. In: Fleming TH, Estrada A (eds) Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer, Boston, pp 15–30

Sodhi NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. Trends Ecol Evol 19:654–660

Stewart KM, Bowyer RT, Kie JG, Cimon NJ, Johnson BK, O'Shea TJ (2002) Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. J Mammal 83:229–244

Sukumar R, Dattaraja HS, Suresh HS, Radhakrishnan J, Vasudeva R, Nirmala S, Joshi NV (1992) Long-term monitoring of vegetation in a tropical deciduous forest in Mudumalai, southern India. Curr Sci 62:608–616

Timmins RJ, Duckworth JW, Samba Kumar N, Anwarul Islam M, Sagar Baral H, Long B, Maxwell A (2008) *Axis porcinus*. In: IUCN 2008. 2008 IUCN red list of threatened species. Available at http://www.iucnredlist.org

Varma S, Pittet A, Jamadagni HS (2006) Experimenting usage of camera-traps for population dynamics study of the Asian elephant *Elephas maximus* in southern India. Curr Sci 91:324–331

Varman KS, Sukumar R (1995) The line transect method for estimating densities of large mammals in a tropical deciduous forest: an evaluation of methods and field experiments. J Biosci 20:273–287

Vellend M, Myers JA, Gardescu S, Marks PL (2003) Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. Ecology 84:1067–1072