Species

Phenological patterns and fruit-frugivore interactions of *Sterculia guttata* Roxb. in a tropical moist deciduous forest of southern Western Ghats, India

VM Thasini[1,2*], VB Sreekumar[1], KA Sreejith[1]

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Author Affiliation:
[1]Forest Ecology and Biodiversity Conservation Division, Kerala Forest Research Institute, Peechi, Thrissur, Kerala 680 653, India
[2]Cochin University of Science and Technology, Cochin, Kerala 682 022, India

[*]Corresponding author
Forest Ecology and Biodiversity Conservation Division, Kerala Forest Research Institute, Peechi, Thrissur, Cochin University of Science and Technology, Cochin, Kerala
India
Email: thasini@kfri.res.in

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ABSTRACT
The observation on phenological patterns and fruit-frugivore interactions of *Sterculia guttata* Roxb. was carried out in the moist deciduous forest of Peechi-Vazhani Wildlife Sanctuary. In *S. guttata*, leaf budding began in March and leaf senescence started in November. Flower budding was initiated in September and fruit setting occurred in October. Fruit maturation happened in January and fruit senescence closely followed the maturation of fruits. At maturity, follicles turn red and dehisce to expose black seeds, which might have attracted frugivores. A total of seven species of birds and two species of mammals were found to feed on the seeds of *S. guttata* during the study period. All the birds swallowed the whole seeds and there was no evidence of seed predation from them. Unlike birds, mammals bit and chewed the seeds and were found to be the major seed predators. Furthermore, these frugivores dropped a large number of seeds under the parent trees while feeding. The present study revealed that *S. guttata* suffered high levels of seed predation, resulting in limited seed dispersal and thereby affecting their survival.

Keywords: Frugivores, Phenology, Seed dispersal, Seed predation, *Sterculia guttata*

1. INTRODUCTION
Plant phenology refers to the timing of plant life-cycle events, such as leaf bud burst, flowering and fruiting. Phenology not only affects the fitness of individual plants, it also affects the fitness of organisms that depend on them (Stucky et al., 2018). In tropical forests, over 90% of woody plant species bear fruits that are consumed and dispersed by animals and a high proportion of animals, especially birds and mammals, feed on fruits (Jordano, 2000; Kissling et al., 2009). Many fruit traits, primarily size, colour and scent, are strongly affected by frugivore trait preference (Valenta and Nevo, 2020). The incidence of pathogens and competition is usually lower at new sites, where the seeds are dispersed by animals (Jordano et al., 2011). Moreover, in forests, animal-mediated seed

dispersal is the main long-distance dispersal mode (Pellerin et al., 2016), which provides the opportunity for gene flow among plant populations (Rubio de Casas et al., 2015). Frugivores also help in the germination success of the seeds by softening the seed coats as they pass through their guts (David et al., 2011). Animals act as both seed dispersers and seed predators; whether this interaction is primarily mutualistic or antagonistic may largely depend on the context (Loayza et al., 2020).

Phenological monitoring provides valuable information on specific events and the production of plant structures (Kasi and Ramasubbu, 2021). Understanding the interactions among fruits and frugivore assemblages is essential not only for animal ecology but also for ecosystem management as their habitat, especially in forest ecosystems (Koike and Masaki, 2019). With this background and perception, we investigated phenological patterns and fruit-frugivore interactions in a deciduous tree, *Sterculia guttata* Roxb. (Malvaceae). This species was earlier reported as zoochorous (Tadwalkar et al., 2012), but no detailed observations on interactions are currently available. This paper chiefly deals with the phenological patterns of *S. guttata*, their potential frugivorous visitors, visitation patterns and foraging behaviours. Finally, we emphasize the need for the conservation of *S. guttata* for the maintenance of biodiversity.

2. MATERIALS AND METHODS

Study area

This study was conducted in the Peechi-Vazhani Wildlife Sanctuary (10^0 28′-$10^0$40′N and $78^0$18′-$78^0$28′E). The terrain is highly rugged and undulating; the altitude ranges from 100 m to 926 m. The sanctuary has a warm humid climate, which is characteristic of the region. The southwest and northeast monsoons are the main sources of atmospheric precipitation in the area. The greater portion of the rainfall in the area is from the southwest monsoon between June and September. The annual rainfall varies between 2500 and 3000 mm. The warm dry wind from mid-November to mid-January accelerates the transition from the wet season to the dry season. The wind is caused due to the tunnel effect, as the sanctuary lies close to the Palakkad gap. The dry months are from December to March. March, April and May are the months when the temperature goes up to about 38^0C in the lowlands and about 32^0C in the hills. During December, January and February, the temperature in the lowlands falls to 21^0C and in the hills, as low as 15^0C.

The major portion of the sanctuary is moist deciduous forests, which occur in the lower elevations and are dominated by trees such as *Bridelia retusa*, *Careya arborea*, *Cassia fistula*, *Dillenia pentagyna*, *Haldina cordifolia*, *Lagerstroemia lanceolata*, *Xylia xylocarpa.* Evergreen forests are found in the higher reaches of the sanctuary and are dominated by trees of *Aporosa lindleyana*, *Canarium strictum*, *Cullenia exarillata*, *Dipterocarpus indicus*, *Dysoxylum malabaricum*, *Hopea parviflora*, *Mallotus philippensis.* Semi-evergreen forests are usually found at relatively lower elevations and occur as a transition zone between moist deciduous and evergreen forests. They are dominated by trees like *Bombax ceiba*, *Cinnamomum zeylanicum*, *Haldina cordifolia*, *Lagerstroemia lanceolata*, *Mallotus philippensis*, *Syzygium cumini*, *Toona ciliata.*

Phenological observations

A total of 10 individuals were marked and monitored for leafing (leaf bud, immature leaf, mature leaf, senescent leaf), flowering (flower bud, immature flower, mature flower, senescent flower) and fruiting (fruit bud, immature fruit, mature fruit, senescent fruit) phenophases. The phenology censuses were made twice in a month from March 2020 to February 2021 by direct visual observation.

Fruit characteristics

Mature fruits were collected and the following characteristics were recorded: follicle length, follicle width, seed number, seed length, seed width, ripe fruit colour and seed colour.

Frugivorous visitors and foraging behaviours

Direct observations were carried out on all fruit-bearing individuals with mature fruits for a period of one week; accessibility of mature fruits was limited due to exploitation by frugivores and also some seeds were found to fall off the open follicles. Observations were done daily from 06.30 to 17.30 hours, during which each tree was scanned continuously for 30 minutes separated by intervals of 1 hour. At each observation, a record of species, their numbers and their foraging behaviours was made. For bird species, information on foraging behaviour included time spent searching and feeding the seeds and the number of seeds swallowed; for mammals, time spent searching and feeding the follicles and the number of follicles dropped, eaten and removed away from parent trees were recorded. It was not always possible to closely observe the foraging behaviour of mammals, as they were shy. Also, in some cases, mammals carried follicles away from parent trees and were obscured by dense foliage. Therefore, the foraging behaviour of mammals was observed opportunistically on all possible occasions. We also tried to quantify the number of seeds dropped by frugivores under parent trees during the feeding process.

3. RESULTS

Observations on vegetative and reproductive phenology

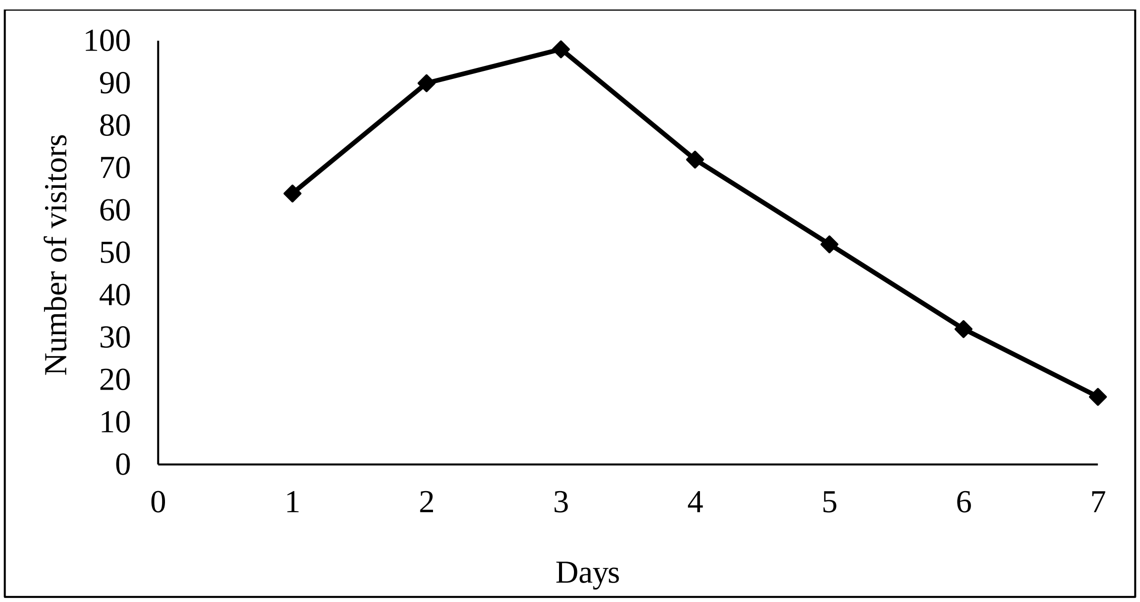
In *S. guttata*, leaf budding began in March and leaf senescence started in November. Of the ten trees monitored for phenology, only four trees flowered and bore fruit. Flower budding was initiated in September and fruit setting occurred in October. Fruit maturation happened in January and fruit senescence closely followed the maturation of fruits.

Fruit characteristics

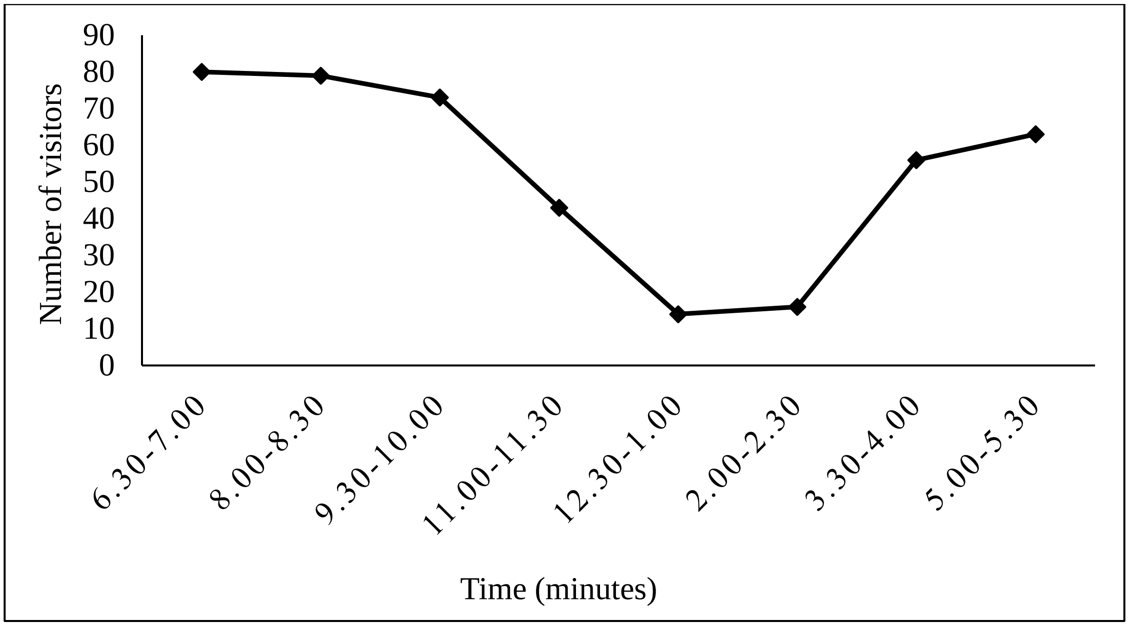
Fruit is an aggregate of 1-5 radiating follicles. Follicle length = 85.02 ± 1.27 mm, follicle width = 57.71 ± 0.50 mm, mean seed number = 9.73 ± 0.47 mm (mean ± SE, n = 30), seed length = 18.19 ± 0.04 mm and seed width = 10.40 ± 0.02 mm (mean ± SE, n = 292). At maturity, follicles turn red and dehisce to expose black seeds.

Frugivorous visitors

A total of seven species of birds and two species of mammals were found to feed on the seeds of *S. guttata* during the study period. The seven species of birds were *Dendrocitta vagabunda* (Rufous treepie), *Gracula indica* (Southern hill myna), *Ocyceros griseus* (Malabar grey hornbill), *Psilopogon viridis* (White-cheeked barbet), *Pycnonotus cafer* (Red-vented bulbul), *Pycnonotus jocosus* (Red-whiskered bulbul), *Sturnia malabarica* (Chestnut-tailed starling) and two species of mammals were *Macaca radiata* (Bonnet macaque) and *Ratufa indica* (Indian giant squirrel). Out of the seven bird species, *S. malabarica* and *D. vagabunda* were more frequent in visits (Table 1). The number of feeding visitors increased from day 1, reached a peak on day 3 and declined thereafter (Figure 1A). Visitation was highest during the morning (6.30 am-11.30 am) and evening (3.30 pm-5.30 pm) hours. In between, they showed a clear reduction in visitation (Figure 1B) and it was seen that most of the individuals were resting in the nearby trees at a maximum distance of 100 m.



A



B

Figure 1 Visitation patterns of frugivores on *S. guttata*: A Number of visitors per day; B Number of visitors per 30 minutes.

Foraging behaviours

The most common foraging behaviour adopted by the birds was searching for the seeds, plucking them with the help of their beaks and swallowing them whole while perching on the branch supporting fruits or on a nearby branch close to fruits (Figure 2). After swallowing the seeds, they normally flew to neighbouring trees in the area and rarely rested in the parent trees. However, the slits in the follicles are relatively small initially, which restricts the easy accessibility of seeds to them. It was found that species differ in their searching and feeding time (Table 1). There was no significant difference in searching time among species (Kruskal-Wallis test; $p > 0.05$), while for feeding time the difference was significant (Kruskal-Wallis test; $p < 0.05$). Among avian visitors, *P. viridis* consumed the maximum number of seeds, followed by *P. cafer*, *S. malabarica*, *D. vagabunda*, *O. griseus*, *G. indica* and *P. jocosus* (Table 1). These differences among the species showed significance (Kruskal-Wallis test; $p < 0.05$). Unlike other birds, *O. griseus* visited trees less frequently but removed a higher number of seeds at each visit, thereby compensating for fewer visits. Birds foraged singly, in groups or in mixed flocks. Interestingly, *O. griseus* was always found to forage singly and *G. indica* in a group of two individuals.

A B

C D

Figure 2 Feeding visits made by birds on *S. guttata*: A *D. vagabunda*, B *O. griseus*, C *P. jocosus*, D *P. viridis*.

Table 1 Foraging observations of avian visitors on *S. guttata* (mean ± SE; n= 56).

Species	No. of individuals	Searching time (s)	Feeding time (s)	No. of seeds swallowed
D. vagabunda	1.68 ± 0.22	23.43 ± 3.02	34.21 ± 4.50	2.29 ± 0.31
G. indica	0.39 ± 0.12	5.18 ±.1.78	11.04 ± 3.36	0.89 ± 0.27
O. griseus	0.25 ± 0.06	4.25 ± 1.12	21.02 ± 5.02	1.61 ± 0.39
P. viridis	1.27 ± 0.18	16.93 ± 2.38	39.59 ± 5.59	3.43 ± 0.49
P. cafer	1.14 ± 0.12	15.86 ± 1.81	36.68 ± 4.07	3.04 ± 0.34
P. jocosus	0.45 ± 0.10	6.45 ±1.55	10.13 ± 2.55	0.82 ± 0.21
S. malabarica	2.02 ± 0.22	28.59 ± 3.11	37.25 ± 4.15	2.48 ± 0.28

The foraging behaviour of mammals contrasted sharply with that of birds. Mammals searched for the follicles and collected them mainly with the help of their mouths and sometimes used their hands and moved to a branch that was convenient to sit and feed. While feeding, they used their hands to hold follicles and their teeth to crush follicles and eat seeds (Figure 3). In some instances, mammals, as that of birds perched on the branch supporting fruits or on a nearby branch close to fruits for feeding. Unlike birds, mammals bit and chewed the seeds. Mammals mainly remained in the fruit-bearing trees to feed. They also carried follicles away from parent trees for feeding, which made it difficult to track them. Group foraging was common in *M. radiata*; a small group of up to four individuals were observed and solitary foraging was recorded only on a single occasion, whereas *R. indica* was a solitary forager and a group of two were observed only on a single occasion.

S. guttata being an aggregate fruit, a large number of follicles were dropped by mammals while plucking each follicle. At each visit, mammals consumed up to 4 follicles and for each follicle they spent 1 to 2 minutes searching and 2 to 3 minutes feeding. *R. indica* were also seen plucking the follicles, eating a few seeds and dropping the rest under the parent trees. Mammals removed a lower number of follicles away from parent trees (Table 2) and we are not sure how many of the seeds were eaten or dropped and thus the fate of the removed follicles remained unclear. In a few instances, the presence of mammals in trees disturbed the visits of birds. However, we found both solitary and group foraging on *S. guttata*. Frugivores also dropped a large number of seeds of *S. guttata* beneath the parent trees due to mishandling of seeds while feeding (Table 3).

Figure 3 Feeding visits made by mammals on *S. guttata*: A *M. radiata*, B *R. indica*.

Table 2 Number of follicles dropped, eaten and removed by mammals during visits recorded in extended watches (n= 56).

Mammals	No. of follicles		
	Dropped	Eaten	Removed
M. radiata	14	43	9
R. indica	18	23	6

*This does not include partially eaten follicles by *R. indica*

Table 3 Seeds dropped by frugivores under parent trees while feeding (n=56).

Species	No. of seeds dropped
D. vagabunda	16
G. indica	14
O. griseus	9
P. viridis	32
P. cafer	19
P. jocosus	12
S. malabarica	14
M. radiata	30
R. indica	37

Of the nine frugivores observed, all the bird species were found to ingest and remove seeds from the vicinity of parent trees before processing them and there was no evidence of seed predation from birds, whereas both mammals ate within trees and they rarely carried follicles away from parent trees. So, the number of seeds dropped away from parent trees can be substantially low. Furthermore, from our ongoing phenological studies on *S. guttata*, we found that considerable quantities of immature seeds were also eaten by these mammals, thus destroying the seeds this way. All these observations implied that birds were responsible for seed dispersal, while mammals were major seed predators.

4. DISCUSSION

Nair et al. (2006) in their study found that the flowering and fruiting period of *S. guttata* is from September to March, whereas in our forest, flower budding was initiated in September and fruit maturation happened in January. Birds are the most important dispersers in the present study and elsewhere (Du et al., 2009; Carlo and Morales, 2016; Zhang et al., 2021). The characteristics of *S.*

guttata related to interaction by frugivores might be that at maturity it has red follicles with black seeds. Studies have confirmed that birds highly prefer fruits with red colour (Larrinaga, 2011; Pires et al., 2018), while mammals feed on fruits of various colours (Bollen et al., 2004; Koike and Masaki, 2019). The sizes of fruits and seeds are limiting factors in interactions between vertebrates and plant species (Sampaio et al., 2018). Our observations also showed that *S. guttata* had a limited avian species assemblage. Tree species may be vulnerable to extinction when they lose their natural seed dispersers (Caughlin et al., 2015). Therefore, the extinction or decline of involved species can affect multiple trophic levels and disrupt ecosystem functions (Keyes et al., 2021).

In the present study, *P. viridis* (White-cheeked barbet) consumed the maximum number of seeds. Barbets were also identified as key frugivores by other workers (Sanitjan and Chen, 2009; Naniwadekar et al., 2019). Next to *P. viridis*, major seed consumers were *P. cafer* (Red-vented bulbul). Bulbuls were established as principal frugivores in Kenya (Schleuning et al., 2011; Menke et al., 2012) and India (Naniwadekar et al., 2019). Swallowing of seeds and moving to neighbouring trees have been observed as common behaviour of birds. Birds that ingest seeds and immediately fly away from the fruiting tree are more likely to be good dispersers (Herrera and Jordano, 1981).

We found that both mammals, *M. radiata* and *R. indica,* are predominantly seed predators but may disseminate seeds indirectly. Our study finding also corroborates that of David et al. (2010), with evidence of *M. radiata* as seed predators and seed dispersers. They noticed full fruits of *Alangium salviifolium* on the ground away from the fruiting tree and added that this was probably carried by the *M. radiata* in their hands and in this way, seeds might be dispersed. A similar situation was reported by Ganesh and Davidar (2005) from Kakachi, while feeding on *Cullenia exarillata, R. indica* may disperse seeds by accidentally dropping them. Frugivores dropped seeds of *S. guttata* beneath the parent trees while feeding, which explains the possibility of long-distance dispersal is limited (Nathan and Casagrandi, 2004). It was seen that mammals ate more seeds at each visit. Such high levels of seed predation have been associated with a lack of other food resources. The number of visitors declined as the day progressed; this could result from reduced accessibility due to fruit depletion.

5. CONCLUSIONS

Our study highlights the position of *S. guttata* as a pivotal resource for frugivores. The low number of fruiting individuals and the dependence of this species on a small assemblage of avian dispersers combined with high levels of seed predation by mammals could have larger consequences on their recruitment and the result would probably be their local extinction. Hence, we emphasize the need for the conservation of this species for the maintenance of biodiversity. As phenological patterns and fruit-frugivore interactions may vary among the forests in India, these kinds of studies need to be replicated in different forest types for better understanding and functioning.

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Authors' contributions

VMT collected the field data and wrote the manuscript under the guidance of VBS and KAS. All authors read and approved the final manuscript.

Ethical approval

In this article, the authors observed the phenological patterns and fruit (*Sterculia guttata* Roxb) - frugivore interactions. The Animal ethical guidelines are followed in the study for species observation, identification & experimentation. Meantime, the ethical guidelines for plants & plant materials are also followed in the study.

Informed consent

Not applicable.

Conflicts of interest

The authors declare that there are no conflicts of interest.

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Data and materials availability
All data associated with this study are present in the paper.

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