**Seed dispersal agents of two *Ficus* species in a disturbed tropical forest**

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Abstract  Observations were carried out at the Bukit Timah Nature Reserve, Singapore on two species of the keystone genus, *Ficus fistulosa* and *F. grossularoides*. This study shows that the two species of different morphological characteristics (e.g. plant height, fruit colour and size) attracted different assemblage of avian frugivores. The frequency of visits by the avian frugivores was significantly different between the two *Ficus* species. The fig-eating frugivore communities feeding on both *Ficus* species seemed to be comparatively depauperate and a substantial number of members were the non-obligate (i.e. routine) avian frugivores. Mammalian frugivory was also observed. The mean number of feedings at *F. grossularoides* might not correlate with body size of the avian frugivores. Such information may aid the forest conservation and management of the nature reserve and future attempts at forest restoration.

Key words  Biodiversity, Conservation, *Ficus*, Frugivory, Fig-disperser declines, Seed dispersal

*Ficus* is one of the largest genus with approximately 350 species in Southeast Asia (Corner 1965). It is widely considered as a keystone mutualist for many vertebrates in the tropical rain forest (e.g. Janzen 1979). Being abundant and always available throughout the year, figs constitute an important diet for many frugivorous animals when other food resources (e.g. insects) are scarce (Leighton and Leighton 1983). It comprises the most important class of plant resources as Terborgh (1986) has shown that the species that feed on the figs constitute about 40% of the animal biomass at Cocha cashu, Peru. Lambert and Marshall (1991) identified the characteristics, which make figs the most important keystone plant resources: their large crop sizes, relatively short fruiting intervals, intra-crown synchrony of fruit ripening and intra-population asynchrony.

The ecological and evolutionary importance of frugivores as seed dispersers in tropical rain forest is well studied (e.g., Estranda and Coates-Estranda 1986; Fleming 1986). The mutualistic relationships between *Ficus* and frugivores are also well known. *Ficus* is heavily dependent on the frugivores to disperse their seeds (Lambert 1989; Lambert 1991). Seed dispersal by animals ensures the long-term survival of many *Ficus* species. Such ecological processes provided by the frugivores may also determine the *Ficus* species and genetic composition in the disturbed landscapes (Corlett 1995; Hamilton 1999). Thus the patterns of visit by frugivores may influence the succession in disturbed areas such as the forest edge or gaps. On the other hand, the presence of fruiting trees in the disturbed landscapes may maintain the frugivorous faunal communities in these areas (da Silva et al. 1996; Restrepo et al. 1999). Understanding such ecological processes is essential for the conservation of biodiversity and restoration of the disturbed landscapes.

In this study we attempted to fill the gaps in knowledge on the fig-eating frugivore assemblage in a disturbed forest habitat. First, we recorded the composition of diurnal vertebrate assembly, feeding on the figs of the two keystone pioneer *Ficus* species, *F. fistulosa* and *F. grossularoides* in a highly isolated, disturbed forest reserve. We compared the species assemblage and visitation pattern in term of frequency and number of fruit consumption, feeding guild and
feeding method of frugivores between the two *Ficus* species. The comparison of the feeding guild and fruit consumption of the visiting frugivores for each *Ficus* species could provide information on their fruit usage and this relates to the importance of figs as a food source. We determined if there was a relation between the frugivore’s body size and the number of figs eaten because it is always assumed that the larger frugivores tend to be more efficient fig dispersers as they consume more figs (e.g. Shanahan et al. 2000). We indirectly examined the relative importance of the observed frugivores for both *Ficus* species based on literature reviews (e.g. Corlett 1998; Shanahan et al. 2000). Lastly, we reviewed the conservation status of resident fig-eating birds of the reserve.

**METHODS**

1) Study site

The study was carried out between 20 January and 24 March 1999 at the Bukit Timah Nature Reserve (hereafter Bukit Timah) in the mainland of Singapore (1°20’N 103°50’E), which situated in a typical equatorial climate. Bukit Timah is a small, isolated forest fragment with the surrounding matrix of urban areas. The 71 ha nature reserve comprises primary hill Dipterocarp forest, which has never been logged, and secondary forest patches of various ages (Corlett 1990). Despite its small size and high human disturbance, Bukit Timah harbours a high floral diversity with more than 800 species of native plants (Corlett 1990). It is also the last primary forest remnant in Singapore where native mammals, birds, reptiles and invertebrates can still be found. The area surveyed was a stretch of forest of secondary nature in the more disturbed part of the reserve.

2) Study subjects

We chose *Ficus fistulosa* and *F. grossularioides* for this study primarily because of their relative abundance. Both members of the *Ficus* are pioneer species, commonly found in the secondary patches of Bukit Timah. They are different morphologically in terms of plant height, fruit size, fruit colour and probably also in their palatability and inherent nutrition. *F. fistulosa* is the taller of the two, reaching a height of 9 m. Its fruits are borne in clusters on woody knobs that line the trunk and main branches. The fruit, of the average diameter of 2.5 cm, are green with white dots, ripening to pale yellow or greenish yellow. *F. grossularioides* is a shrub-like or small tree that reached a maximum of 3 m. Its fruits have an average diameter of 1.25 cm. Those are sessile, round and are mostly on twigs just below the leaves. Those ripen from yellow to brownish ochre to dark red. Descriptions of the two *Ficus* species are derived from Ng (1978).

3) Focal observations and statistical analyses

We conducted an observation for 12 days between 0700 h and 1000 h when the frugivores are most actively feeding in the morning. Different fruiting trees of both *Ficus fistulosa* and *F. grossularioides* were sampled for each morning session. Thus 12 trees with a total of 18 h of observation were performed for each *Ficus* species. For every session, we chose one fruiting tree of each *Ficus* species, of which at least half of their crown visible from the ground, for focal watch. The observations were carried out in 15 min blocks that alternated between the two species. Binoculars (8×30) were used to aid in identification of the feeding frugivores. Identification of the avian and mammalian frugivores followed King et al. (1989) and Lekagul and McNeely (1988) respectively.

Frugivores foraging in the fruiting *Ficus* trees were recorded and grouped accordingly to their feeding guilds: animals that are obligate frugivores feed mainly on fruits and routine frugivores have a wide range of mixed diet. Foraging habits of the frugivores in the fruiting *Ficus* were also observed and classified into three feeding methods following Trainer and Mill (1984): species that are “swallowers” took the figs as a whole, “marshers” that squashed the figs in the beaks before swallowing the whole or most of the fruit, and “biters” that pecked at the fruit, feeding on the figs in small bits.

We noted the number of fruit eaten by the visiting frugivores. The taking of a whole fruit or any removal of the fruit in small section was counted as a feeding. When it was not obvious if the animal had fed on some fruit, the head-pecking movements were counted as well. We used Spearman-ranked correlation test to determine if there was any relation between the mean number of figs eaten by the “swallowers” and their body sizes. Body sizes of the frugivores were obtained from Robson (2000). All data are analysed using Statistical Analysis System (SAS). Invertebrates, like ants and other insects, were not included in this study. Another important group of frugivores, fruit bats, was also not dealt with.
4) Fig-eating bird assemblage

We compiled a checklist of forest resident fig-eating birds of Bukit Timah, from pre-1940 to 1991, based on literature research (e.g. Lim 1992; Shanahan et al. 2000) and personal observations. The conservation status of these fig-eating frugivores in Bukit Timah was reviewed according to Lim (1992). The quality of the fig seed dispersers was difficult to judge and was based on a review paper by Corlett (1998). The nomenclature of avian and mammalian frugivores followed Inskipp et al. (1990) and Corbet and Hill (1991), respectively.

RESULTS

1) Birds

A total of 15 bird species were spotted feeding on figs of both Ficus species (Table 1). Four species of birds were observed feeding on figs of F. fistulosa whereas 14 species were seen on F. grossularoides. We observed eight individuals belonging to three resident and one introduced species on F. fistulosa. The most common species seen feeding on the figs of F. fistulosa was the Pink-necked Pigeons. We found 34 individuals belonging to 13 resident and one migrant species feeding on the figs of F. grossularoides. The Pink-necked Pigeons were the most common frugivores for F. grossularoides, followed by the Yellow-vented Bulbul and White-vented Myna. The common species that fed on both Ficus were the Pink-necked Pigeons, Black-naped Orioles and Asian Glossy Starlings. More species of avian frugivores were observed feeding on F. grossularoides than on F. fistulosa ($\chi^2=6.20$, P<0.05). Similarly, more individuals were seen feeding on F. grossularoides than on F. fistulosa ($\chi^2=16.12$, P<0.01).

The average number of feedings by all avian “biter” species for F. fistulosa ranged from three to five pecks per visitation (Table 1). The only “swallower” for F. fistulosa, the Great Hornbill, was observed to consume eight figs during its one-timed visitation. The biters for F. grossularoides comprised three species, which had an average of two to six mean feedings per visitation. The average number of feedings for F. grossularoides by the “swallowers” species (12 species) ranged from two to nine figs per visit. For F. grossularoides, one Asian Fairy Bluebird was observed to swallow the most number of fruits, a total of 9 figs during its visitation.


<table>
<thead>
<tr>
<th>Species</th>
<th>Feeding guilds</th>
<th>Ficus fistulosa</th>
<th>Ficus grossularoides</th>
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<td>Feeding Methods</td>
<td>N visits</td>
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<tr>
<td>Birds</td>
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<td>Routine Swallower</td>
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<td>Red-crowned Barbet Megalaima rafflesii</td>
<td>Obligate</td>
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<tr>
<td>Coppersmith Barbet Megalaima haemacephala</td>
<td>Obligate</td>
<td></td>
<td></td>
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<td>Pink-necked Pigeon Treron vernans</td>
<td>Obligate Biter</td>
<td>4</td>
<td>5.0</td>
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<tr>
<td>House Crow Corvus splendens</td>
<td>Routine</td>
<td></td>
<td></td>
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<tr>
<td>Scarlet-backed Flowerpecker Dicaeum cruentatum</td>
<td>Routine</td>
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<tr>
<td>Orange-bellied Flowerpecker Dicaeum trigonostigma</td>
<td>Routine</td>
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<td>Asian Fairy Bluebird Irena puella</td>
<td>Obligate</td>
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<td>Black-naped Oriole Oriolus chinensis</td>
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<tr>
<td>Yellow-vented Bulbul Pycnonotus goiavier</td>
<td>Routine</td>
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<td>Olive-winged Bulbul Pycnonotus plamnosus</td>
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<td>White-vented Myna Acridotheres javanicus</td>
<td>Routine</td>
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<td></td>
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<tr>
<td>Asian Glossy Starling Aplonis panayensis</td>
<td>Obligate Biter</td>
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<td>Short-tailed Babbler Trichastoma malaccense</td>
<td>Routine</td>
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<td></td>
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<td>Eye-browed Thrush Turdus obscurus</td>
<td>Routine</td>
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<tr>
<td>Mammals</td>
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<td></td>
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<td>Common Treeshrew Tupai a glis</td>
<td>Routine Biter</td>
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<tr>
<td>Long-tailed Macaque Macaca fascicularis</td>
<td>Obligate Marsher</td>
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<td>X</td>
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<tr>
<td>Plantain Squirrel Callosciurus notatus</td>
<td>Routine Biter</td>
<td>5</td>
<td>2.8</td>
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</table>
2) Mammals

Three species of mammals were found to be feeding on the figs of one or both *Ficus* species (Table 1). They were the Common Treeshrews, Long-tailed Macaques and Plantain Squirrels. We observed 12 individuals belonging to three mammalian species feeding on the figs of *F. fistulosa* but recorded only three Plantain Squirrels feeding on *F. grossularoides*. Thus, more individuals of mammals were observed feeding on *F. fistulosa* than on *F. grossularoides* ($\chi^2=5.46, P<0.05$). The most common mammal eating the figs of *F. fistulosa* was the Long-tailed Macaques.

The average number of feedings by the Plantain Squirrels for *F. fistulosa* and *F. grossularoides* are 2.8 and three per visitation, respectively (Table 1). The data for other species was unable to obtain because poor visibility hampered the observation.

3) Feeding guilds, Foraging methods and Body sizes

The relative abundance of non-obligate (i.e. routine) frugivore among the vertebrate assembly was substantial for both *Ficus* species (Fig. 1). Only three species, which comprised 11 individuals, were considered as obligate frugivores among the species assembly for *F. fistulosa*. The obligate frugivores feeding at *F. grossularoides* included four species of a total of 14 individuals. The numbers of obligate frugivores (including mammals) between both *Ficus* species are not significantly different ($\chi^2=0.4, P>0.01$). However, more obligate avian frugivores were observed feeding at *F. grossularoides* than at *F. fistulosa* ($\chi^2=4.31, P<0.05$).

More “swallowers” were observed feeding on *F. grossularoides* whereas the consumers for *F. fistulosa* were mostly “biters” (Fig. 2). There was an absence of “marshers” on *F. grossularoides*. For the avian frugivores that swallowed figs of *F. grossularoides*, we found that there was no correlation between the number of fig eaten and their body sizes (Spearman-ranked correlation = 0.373, $P>0.05$).

4) Fig-eating bird assemblage

46.2% of the 65 resident avian fig-eating species from 17 families recorded since pre-1940 still persist in Bukit Timah. Of the remaining 30 species, 66.7% are considered to be of high quality fig-seed dispersing (HQFD) species which are more efficient at seed dispersal. However only nine species are HQFD forest specialists and all of them are classified locally as threatened species (Table 2). The more important avian fig-eating families at Bukit Timah in term of the number of genera and species eating figs are Pycnonotidae, Irenidae, Corvidae, Nectariniidae, Cuculidae and Lybiidae. We observed 10% of the total HQFD species assemblage feeding on figs of *F. fistulosa* and 4% of that on *F. grossularoides* (excluding winter migrants, reintroduced and non-native species).

**DISCUSSION**

Comparison between *F. fistulosa* and *F. grossularoides* shows the difference in frugivore diversity. Both species exhibit different characteristics, which attracted different assemblage of diurnal frugivores.
The potential primary dispersal agents for *F. fistulosa* are mainly terrestrial mammals and bats (Lambert 1991). Its figs are too large for most avian frugivores to swallow as a whole. Although the fruits of *F. fistulosa* do not show any of the typical bird-dispersal syndromes described by van der Pijl (1972), they caught the attention of some relatively larger birds such as the Great Hornbill and Pink-necked Pigeons and also 10% of the total HQFD species assemblage at Bukit Timah. This showed that *F. fistulosa* fits into the description for tropical *Ficus* species associated with generalist nature of the disperser assemblage. The contribution of individual frugivore species varied considerably. The HQFD species observed feeding in *F. fistulosa* were the Black-naped Oriole, Asian Glossy Starling and Long-tailed Macaque. Since half of the recorded avian visits were pink-necked pigeons, this seed predator exhibited a pattern of dominance in avian fig-eating assemblage to *F. fistulosa*.

On the other hand, *F. grossularoides* were visited by a wider range of fig-eating birds even though Lambert (1989) reported that there was no bird feeding on the figs of *F. grossularoides* at Kuala Lompat, Malaysia. Although *F. grossularoides* exhibits typical bird dispersing qualities in fruit size, colour and asynchrony in ripening, its figs are also readily consumed by the Short-nosed Fruit Bats, *Cynopterus* spp. (Ling Ong, pers.com). Most of the avian frugivores swallowed the figs except the smallest flowerpeckers that pecked the fleshy tissues of the figs. The HQFD species observed on *F. grossularoides* were the Red-crowned Barbet, Coppersmith Barbet, Scarlet-backed Flowerpecker, Orange-bellied Flowerpecker, Asian Fairy Bluebird, Yellow-vented Bulbul, Olive-winged Bulbul and Asian Glossy Starling. The Pink-necked Pigeons and Yellow-vented Bulbuls dominated the fig-eating assemblage. Most of these species are the smaller frugivores, which are not obligate fig-eaters. Nevertheless, these small generalists are important for the fig seed dispersal as our results suggested that the number of figs eaten might not correlate with body sizes of the birds.

Only nine avian HQFD species at Bukit Timah are forest specialists that frequent in relatively undisturbed part of the reserve, and all of them are classified as locally threatened species. They are the Red-crowned Barbet, Drongo Cuckoo, Blue-winged Leafbird, Lesser Green Leafbird, Greater Green Leafbird, Asian Fairy Bluebird, Yellow-vented Flowerpecker, Red-eyed Bulbul and Cream-vented Bulbul. The declines of the fig-eating frugivores at Bukit Timah since 1800s no doubt limited the number of species

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**Table 2.** Contributions of families to total number of high quality fig dispersing (HQFD) species in Bukit Timah from pre-1940 to 1991. The quality of the fig dispersers was based on Corlett (1998). Migrants and non-native species were not included.

<table>
<thead>
<tr>
<th>Families</th>
<th>Total fig dispersers (N)</th>
<th>Extinct species (N)</th>
<th>Extant HQFD (N)</th>
<th>HQFD forest specialists (N)</th>
<th>Threatened HQFD forest specialists (N)</th>
<th>Proportion of HQFD in relation to total extant fig dispersing species (%)</th>
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feeding on both *F. fistulosa* and *F. grossularoides*. The absence of more important fig-seed dispersers at Bukit Timah may lead to a dominance of small generalist (routine) frugivores that are more tolerant to fragmentation and able to switch diets opportunistically in their altered landscapes (Table 1; Fig. 2). The only avian HQFD forest specialists contributed to the recorded visits were the Red-crowned Barbet and Asian Fairy Bluebird. The loss of HQFD species in biotic communities may have an irreversible effect on the stability, functioning and sustainability of an ecosystem (Tilman 1997). Bukit Timah serves as a forecast of what may happen to fig-eating frugivores as a result of habitat disturbance and fragmentation. It also reflects a trend of global declines for individual species and populations of fig-eating frugivores. Excluding fig-eating reptiles and fishes, about 18% of all bird and mammal species known to eat figs are either at risk or near threatened at a global level (Peh K.S.-H., unpublished data).

Although habitat destruction and fragmentation have been identified by many studies as root causes of the current global biodiversity crisis and conservation problems (e.g. Turner 1996; Debinski & Holt 2000), serious threats faced by fig-eating frugivores include disturbance of roost sites, poaching, introduction of alien predators, harmful effects of environmental pollution and unpredictable natural disturbances such as hurricanes. All cases of threats have the potential to result in the local loss of fig-eating species. Efforts to address the issues of fig-eating frugivores' declines in disturbed habitats are very much needed. Information on the interaction patterns among fig-seed dispersers and *Ficus* in rain forests with respect to community structure, degree of generalization or specialization of interactions, and ecosystems health may be vital for forest conservation and management of small reserves. Such knowledge may also aid in any future attempts in rain forest restoration.

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