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Seed Dispersal by the Lesser Short-nosed Fruit Bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera)

PHUA POH BOON¹ AND RICHARD T. CORLETT²

Abstract: *Cynopterus brachyotis* is a very common, medium-sized (37 gm) fruit bat in Singapore. Information on feeding habits was obtained by direct observation of wild bats, collection of seed and fruit remnants under feeding roosts, netting wild bats and collecting faeces samples, and observing caged bats. Seed fate is determined by fruit weight, seed dimensions and fruit texture. Fruits < 20 gm are usually carried off to a feeding roost for processing. The smallest seeds (< 2.3 mm length) are swallowed and subsequently defecated in flight or while roosting. Larger seeds are dropped undamaged under feeding roosts.

INTRODUCTION

The Lesser Short-nosed Fruit Bat (*Cynopterus brachyotis*) is probably the commonest and most widespread fruit bat in tropical Asia (Lim, 1966; Lekagul and McNeely, 1977; Medway, 1978). It occupies most available habitats: coastal, urban, agricultural, riverine and all types of forest up to 1500 m altitude. *C. brachyotis* is a medium-sized bat (mean 37.3 gms, $n = 10$, in Singapore) which typically roosts in small groups in trees, particularly under the fronds of palms. From the sparse and largely anecdotal literature, it appears to be an important seed-dispersal agent (Ridley, 1930; Doctors van Leeuwen, 1935; Pijl, 1957, 1982). It also feeds on nectar and may be important in pollination (Gould, 1978; Medway, 1978). The aim of our study was to investigate the influence of seed and fruit characteristics on the potential for seed dispersal by *Cynopterus brachyotis*. Plant names follow Keng (1973–85): animal names follow Medway (1978).

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The study was carried out in Singapore, which has an equatorial climate with no dry season. Most work was done in young secondary forest on the campus of the National University of Singapore or at the Singapore Botanic Gardens. These sites were chosen because their floras are well known and their openness made observation easier. Limited observations were also made in other habitat types.

Information on the feeding habits of *Cynopterus* was obtained in four ways: by direct observation of wild bats; by collection of seeds and fruit remnants dropped under feeding roosts; by offering a variety of fruits to captive bats and observing their behaviour. Direct observation of small bats at night is difficult, but confirmed the identification of feeding roosts — places, usually trees, to which the bats flew with fruit before consuming it. The major feeding roosts studied were all in the Botanic Gardens and were also used as daytime roosts. Bats were netted with mist nets placed across observed flight paths. A total of 51 *C. brachyotis* were caught, all on the University campus in the vicinity of young secondary forest. Faeces samples were collected from plastic sheeting placed under the nets and by placing the capture bats in a cage for at least 30 minutes. Plastic sheeting was also placed under flight paths to detect defecation in flight. For the feeding experiments, up to 6 bats were kept together in a wire mesh cage. Fruits were offered in petri dishes, either in the evening or in a darkened, air-conditioned room during the day, and the feeding behaviour observed in detail.

For all the fruits eaten by *Cynopterus* that could be obtained intact, seed number, seed dimensions, fruit weight, and general morphological characteristics were determined. The fresh weights of the largest fruits carried to feeding roosts were estimated from seed size by regressions of fruit weight on seed size for freshly-collected fruit.

RESULTS

Table 1 summarizes the observations on the fate of the seeds in fruits eaten by wild and captive *Cynopterus*. The wild *Cynopterus* ate a wide variety of fruits during the period of the study: both soft- and hard-fleshed, protected (with inedible rind) and unprotected, and with a wide range of seed and fruit sizes and seed numbers. Most of those eaten by wild bats had more or less cryptic coloration (green, brown or purplish), although there were exceptions, and most were displayed clear of the foliage. Captive bats ate some species that may not have been eaten by wild bats.

The fate of the seed or seeds seemed to be determined largely by the weight of the fruit and the dimensions of the seeds. Fruits up to about 20 g

METHODS

Table 1. Fruit and seed morphology, and seed fate for species eaten by *Cynopterus brachyotis*. In order of seed size.
Seed fates from experiments with caged bats unless indicated otherwise.

Species	Family	Fruit ^a type	Fruit colour	Fruit wt. (g)	Seed dimensions (mm)	Seed fate	
<i>Muntingia calabura</i>	Elaocarpaceae	U, S	red	0.84	0.6	0.4	swallowed
<i>Fagraea fragrans</i>	Loganiaceae	U, S	red	0.8	0.8	0.8	swallowed
<i>Ficus fistulosa</i>	Moraceae	U, S	green	3.04	1.6	0.8	swallowed
<i>Pellacalix saccardianus</i>	Rhizophoraceae	U, S	green	1.99	1.7	1.2	swallowed
<i>Adinandra dumosa</i>	Theaceae	U, S	green	1.52	2.2	1.4	swallowed
<i>Cecropia peltata</i>	Cecropiaceae	U, S	green	4.88	2.4	1.1	spat in clumps
<i>Psidium guajava</i>	Myrtaceae	U, H	green	68.15	3.6	2.9	spat in clumps
<i>Vitex pinnata</i>	Verbenaceae	U, S	black	0.35	5.0	4.8	spat singly
<i>Campnospermum auriculatum</i>	Anacardiaceae	U, S	purple	0.82	5.5	4.8	spat singly ^b
<i>Musa</i> sp.	Musaceae	P, S	yellow	C. 10	7.8	6.9	spat singly
<i>Eugenia longiflora</i>	Myrtaceae	U, S	white	0.90	7.8	6.7	spat singly
<i>Nephelium malaiense</i>	Sapindaceae	P, S	brown	4.42	12.0	11.9	spat singly
<i>Podocarpus rumphii</i>	Podocarpaceae	—	red	4.72	16.6	14.1	dropped singly
<i>Palaquium gutta</i>	Sapotaceae	U, S	brown	6.20	17.2	13.1	dropped singly
<i>Palaquium obovatum</i>	Sapotaceae	U, S	brown	4.10	18.8	11.0	dropped singly
<i>Diospyros</i> sp.	Ebenaceae	P, S?	green	C. 10	19.9	9.8	dropped singly ^b
<i>Eugenia jambos</i>	Myrtaceae	U, S	green	8.01	20.2	16.9	dropped singly
<i>Eugenia grandis</i>	Myrtaceae	U, H	green	10.75	20.8	17.6	dropped singly
<i>Calophyllum inophyllum</i>	Clusiaceae	U, H	green	11.90	25.3	24.6	dropped singly
<i>Eugenia malaccensis</i>	Myrtaceae	U, S	red	7.87	30.5	19.0	dropped singly
<i>Terminalia catappa</i>	Combretaceae	U, H	green-yellow	14.16	39.0	25.1	dropped singly

a U = unprotected, P = with inedible rind, S = soft, H = hard

b Seed fates deduced from field observations.

were usually carried away to feeding roosts for processing. The estimated fresh fruit weight of the largest *Terminalia catappa* seed found under a feeding roost was 20.25 g. Most fruits were carried off singly but with *Fagraea fragrans*, the smallest fruit eaten, several fruits were plucked and carried off together. The same behaviour was observed when the 6–8 mm diameter fruits of *Camponospermum auriculatum* (not definitely eaten by wild bats) were offered to caged bats. Larger fruits were eaten while attached to the parent tree. In the case of *Psidium guajava*, the largest fruit eaten, mouthfuls of flesh with seeds were carried off for processing.

Processing involved several steps depending on fruit size and morphology. Larger fruits were held against the body by a hind leg and bites were taken from the fruit after removing the rind, if present. Smaller fruits were taken whole into the mouth. In all cases, only fluid and smaller particles were swallowed and the skin and fibrous components of the flesh spat out. Only the smallest seeds (less than 2.5 mm long and 1.5 mm wide) were ever swallowed and appeared in the faeces: larger seeds were dropped undamaged under the feeding roost. Seeds larger than 5 mm long were spat out singly, or dropped after cleaning outside the mouth, while two species of intermediate size were spat in tight clumps with fruit remnants. For small-seeded fruits, the proportion of seeds swallowed was greatest for those with semi-fluid interiors (e.g. *Adinandra dumosa*, *Muntingia calabura*). *Cecropia peltata* seeds were apparently never swallowed, despite being narrower and slightly longer than seeds of *Adinandra*, perhaps because of the dryer and firmer fruit texture.

Swallowed seeds were defecated in flight and while roosting. The faeces consisted of fruit pulp and seeds, with no visible change as a result of digestion. The faeces are not cohesive so the seeds spread out in the air and fall separately. Passage times in captive bats ranged from 11 to 15 minutes. Faecal samples were obtained from 40 bats netted in the University. Of these, 39 contained only seeds of *Adinandra dumosa* — the dominant species in the adjoining secondary forest — and the other only seeds of *Muntingia calabura*. A total of 389 seeds were collected from plastic sheeting under bat flight paths: 92.8 percent *A. dumosa* and the rest *Fagraea fragrans*.

The feeding roosts were usually within 100 m of the fruiting tree. Occasionally fruits were certainly carried much further, but as the distance increased it became more difficult to identify the source tree with certainty. Almost any tree with horizontal branches more than 3 m above the ground might be used as a feeding roost but the preferred roosts, where available, were palm trees with fan-shaped leaves. These were often used also as daytime roosts. The most favoured species in the Botanic Gardens was *Corypha uata*, which sometimes supported colonies of 100 or more bats. The bats construct 'tents' by chewing through the veins, causing the collapse of the distal area of the leaf, as described for *Cynopterus sphinx* in Timor (Goodwin, 1979).

Adinandra dumosa was by far the most important species in the diet at the University, on the evidence of night observations, faecal samples and discarded fruit remnants under temporary feeding roosts. The diet of the bats at the Botanic Gardens was more varied, but *Eugenia grandis* was clearly the preferred food when available and figs were dominant when it was not. At least 6 species of *Ficus* were eaten but most could not be identified with certainty from the fragmentary remains. Surprisingly, the fruit remnants under feeding roosts often included partly-eaten, seedless 'gall figs' of the dioecious *F. fistulosa* (sometimes with fig wasps still emerging) and occasionally other species. The red, sweet and juicy seed figs of *F. grossularioides* were rejected by captive bats.

One surprising item in the diet of the Botanic Garden bats was the 'fruit' of the conifer *Podocarpus rumphii*. The fleshy red receptacle with attached seed was carried off to a feeding roost, where the receptacle was eaten and the seed dropped. The colour and position (buried among the foliage) of the fruit suggest that *P. rumphii* is usually bird-dispersed, but it formed a major part of the diet of nearby colonies while it was available. Other interesting choices were the fruit of *Cecropia peltata* and *Muntingia calabura*, pioneers dispersed by unrelated microchiropteran bats in their native tropical America (Fleming, 1982).

DISCUSSION

The results suggest that *Cynopterus brachyotis* may be a very important seed dispersal agent, at least in the open habitats studied. Extrapolation to closed forest requires further study. The quality of seed dispersal provided depends on seed and fruit characteristics. The bats' habit of defecating in flight provides high quality dispersal for small-seeded, light-demanding pioneers. *Adinandra dumosa* is the dominant pioneer on abandoned, degraded agricultural land in Singapore and the southernmost part of the Malay Peninsula. Its green fruits, displayed clear of the foliage, are produced continuously throughout the year and are apparently never taken by birds, and rarely by other mammals. This phenology ensures regular visits by *C. brachyotis* and, at least since human disturbance greatly increased its abundance, *A. dumosa* must be a major factor in maintaining high density bat populations. It would seem likely that the tree architecture, fruit morphology and reproductive phenology of *Adinandra* have evolved in response to selection for dispersal by *Cynopterus* and similar medium-sized fruit bats. Janzen (1983) suggests that the major stumbling block to tight plant-disperser coevolution is that few plants maintain a year-round crop of fruits of sufficient quantity and quality to sustain a vertebrate population. *Adinandra* may be an exception. *Fagraea fragrans* is also common as a pioneer on degraded sites but its scarlet fruits are also eaten by a few species of bird, although most ignore it. The fruits of two other pioneers,

- Rhodamnia cinerea* and *Vitex pinnata*, were eaten by caged bats but we have only seen birds eating them in nature. Perhaps surprisingly, in view of the success of *Adiantum*, most other pioneer species in Singapore seem to be dispersed by birds.
- Larger seeds are mostly dropped under favoured feeding roosts, where their high density must make them almost as vulnerable to pests and disease as those dropped under the parent tree. However, some seeds of all species are dropped in low densities under minor roosts and a few are dropped — usually as partly eaten fruits — in flight in the open. *C. brachyotis* may thus be an important dispersal agent for these species, too. Many of the dominants of older secondary forests in Singapore (e.g. *Calophyllum* spp., *Elaeocarpus* spp., *Eugenia* spp.) may, on morphological grounds, be largely dispersed by *C. brachyotis*.
- The only other fruit bat seen in Singapore during this study was the very much larger flying fox, *Pteropus vampyrus* (850 g). Although potentially capable of carrying off much larger fruits than *C. brachyotis*, this species seems to be far more arboreal, tending to land in the canopy of large fruiting trees and climb about eating fruit. The seeds are thus less likely to be carried away from the tree.
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