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Fig-eating by birds in a Malaysian lowland rain forest

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ABSTRACT. Sixty bird species ate the figs of 29 Ficus taxa at a lowland forest site in Peninsular Malaysia. Although most bird-eaten figs were brightly coloured, four Ficus species produced dull-coloured ripe fruits. Whilst there was tremendous overlap in the sizes of figs eaten by different bird species, data presented show that the fig resource was partitioned by birds. Large birds were commoner visitors to large-fruited Ficus, but small birds tended to eat small figs. Within two avian genera, the Treron pigeons and Megalaima barbets, there was distinct partitioning of figs consumed according to fig size.

KEY WORDS: birds, Ficus, figs, frugivory, Malaysia, Megalaima, rain forest, resource partitioning, seed-dispersal, Treron.

INTRODUCTION

There are many accounts, both anecdotal and systematic, of the diverse assemblages of frugivores, particularly birds, that feed on ripe figs in the tropics (Breitwisch 1983, Brockelman 1982, Coates-Estrada & Estrada 1986, Jordano 1983, Kantak 1979, Lambert 1987, Leighton 1982, McClure 1966, Pratt 1983, Pratt & Stiles 1985, Ridley 1930, Scott & Martin 1984, Snow 1980, Snow & Snow 1971, Terborgh & Diamond 1970, Wells 1975, 1982, Wheelwright *et al.* 1984). Indeed, figs constitute a larger proportion of the diet for more vertebrate species than the fruits of any other tropical perennial plant genus (Janzen 1980).

Despite the poor nutritional quality of figs (Frost 1980, Herrera 1981, Leighton 1982, in press, Morton 1973, White 1974), they play the very important role of sustaining frugivorous animals through periods when alternative fruit resources are scarce in at least two tropical forest areas (Leighton & Leighton 1983, Terborgh 1986). Whilst the well documented aseasonal fruiting phenology of *Ficus* (e.g. Corlett 1984, McClure 1966, Medway 1972, Raemaekers *et al.* 1980) is the overriding trait which enables *Ficus* to fulfil this role, several other factors of *Ficus* fruitings also make essential contributions. Thus the enormous crop sizes, distinctive intra-crown synchrony of fruit ripening, the relatively short intervals between fruiting by individual trees and the ease with which figs can be harvested by diverse assemblages of frugivores are all

important fruiting traits which contribute to the unique role that *Ficus* plays in frugivore survival (Lambert 1987).

In Malaysian forests one other attribute of *Ficus* also contributes to the importance of *Ficus* to frugivores; *Ficus* are abundant, being the second commonest genus after *Eugenia* (Ng 1978). There are at least 101 species of *Ficus* in Peninsular Malaysia (Ng 1978), and typical densities of mature *Ficus* in low-land forests are 2-3 plants per hectare (Johns 1983, Lambert 1987).

Despite the abundance of *Ficus*, and the recognition that *Ficus* is of exceptional importance to frugivores in Old World forests, there has been no systematic recording of the disperser assemblages of *Ficus* taxa at a single site. This paper identifies the fig-eating bird species associated with *Ficus* and the figs that they eat, at a lowland forest site in Peninsular Malaysia.

STUDY AREA AND METHODS

The study area, Kuala Lompat (3° 43′ N, 102° 17′ E), lies at the south-eastern periphery of the Krau Game Reserve, Malaysia, at the confluence of the rivers Krau and Lompat. The area is relatively flat, mostly at elevations of 50-80 m, although further west the terrain becomes more hilly as it rises towards Mount Benom. Whilst most of the vegetation within the Game Reserve is climax forest, the Kuala Lompat area exhibits signs of limited disturbance. There are two manmade clearings, designed to attract ungulates, at the edge of the study area. The vegetation has been described as lowland evergreen dipterocarp forest, although it is relatively poor in dipterocarps, and unusually rich in large leguminous trees (Raemaekers et al. 1980). At Kuala Lompat all observations were made within a 2.1 km² patch of forest. Additional observations were made at a fruiting Ficus virens at Taman Negara National Park, some 90 km north of Kuala Lompat. The avifauna and vegetation of Taman Negara are very similar to that at Kuala Lompat, although the terrain is more hilly. Further descriptions of the Kuala Lompat study area can be found in Chivers (1980) and Lambert (1987). The avifauna of the site has been partially reported by Medway & Wells (1971).

Voucher specimens of leaves and fruits were used to identify *Ficus* species by comparison with labelled herbarium material. Fruit characters were assessed in the field, from freshly fallen figs or, when possible, from fruits from the tree. Callipers were used to measure fruit lengths and diameters of representative samples of fruits.

More than 750 hours of observations were made of fruiting *Ficus* within the study area between March 1984 and October 1986. In all instances trees were chosen for observation only if at least half the fruiting crown could be observed, either from the ground, or from a platform which could be moved to suitable locations and elevations in the forest. Observation periods usually lasted three hours, and were timed to sample different periods of the day. However, few observations were made within the first half hour of day break due to a curfew imposed by the army. Observation periods consisted of continuous series of

ten-minute intervals during which all visitor species, and an estimate of their number, were recorded.

RESULTS

Ficus taxa with bird-eaten fruit

Thirty-eight *Ficus* taxa were identified at Kuala Lompat, of which 29 taxa had fruits regularly eaten by birds (Table 1). All taxa with figs eaten by birds were stranglers or scrambling epiphytes (three species: *F. recurva, F. sagittata,*

Table 1. Ficus taxa of Kuala Lompat. Species with fruits eaten by birds are indicated by a bold dot. Mean size (length × width) and colours of ripe fruits are indicated where known. CD: Ficus species code used in other tables and figures. Taxonomy follows Corner (1965).

CD	Species	Size (mm)	Colour
	• F. sinuata*	4.4×4.0	Red
	• F. caulocarpa	5.4×5.9	Pink/pale yellow
	• F. sumatrana	5.7×7.6	Dull pink/ochre
	• F. virens	7.0×7.7	Greenish/ochre
5	• F. obscura*	7.1×7.8	Red/deep red
6	• F. recurva *	Small	Red
7	• F. heteropleura*	7.6×7.7	Red
8	• F. binnendykii	8.5×7.8	Pink/purple
9	• F. benjamina	8.9×7.6	Pink/purple
10	• F. subulata*	10.2×10.4	Red
11	• F. delosyce	10.1×11.0	Pink/yellow-green
12	• F. pisocarpa	11.6×12.3	Yellow-orange
13	• F. sagittata*	12.0×12.0	Red/deep red
14	F. grossularioides	12.5×12.2	Dull orange
15	• F. kerkhovenii	13.3×11.9	Orange-red/red
16	• F. pellucido-punctata	17.7×11.6	Purple
17	• F. parietalis*	14.8×15.4	Red
	• F. sundaica (type 2a)†	14.4×16.7	Red/deep red
19	• F. stricta	15.8×15.7	Red
20	• F. consociata	14.3×17.8	Red/deep red
21	• F. trichocarpa*	15.5×17.5	Deep red
	• F. sundaica (type 1)†	16.6×16.8	Red/deep red
23	• F. crassiramea	20.0×17.5	Red/deep red
24	• F. sundaica (type 2b)†	19.6×18.3	Red/deep red
25	F. variegata	21.2×18.1	Red/purple
26	• F. bracteata	18.5 imes 21.5	Red
27	F. globosa	Medium-large	Dull
28	F. $annulata$	28.7×22.2	Brownish
29	• F. cucurbitina	30.9×20.3	Deep red/black
30	• F. dubia	28.6×27.6	Deep red/purple
	• F. stupenda	32.4×27.4	Red/deep red
32	F. depressa	35.1×26.4	Brownish
33	F. obpyramidata	Large	Brown
	• F. drupacea	36.4×27.7	Deep red/purple
35	• F. subcordata	45.5×34.8	Red
36	F. aurantiacea	69.5×68.4	Black
37	F. punctata	77.0×70.0	Deep purple
38	F. vrieseana‡	Unknown	Unknown

^{*} Gynodioecious species: only fruits of female trees eaten by birds.

[†] The three F. sundaica taxa are described in Lambert (1987).

[‡] Caulocarpous: figs unlikely to be eaten by birds.

F. trichocarpa). Although birds consumed figs from both ends of the size spectrum, the huge (c. 70 mm diameter) figs of F. aurantiacea were rarely eaten. Two species of hornbill (Pied Hornbill Anthracoceros albirostris and Black Hornbill A. malayanus) and one flowerpecker (Crimson-breasted Flowerpecker Prionochilus percussus) were observed eating pieces from the ripe fruits of F. aurantiacea outside the forest, but avian consumption of this fruit within the forest was never observed.

The majority of bird-eaten figs were brightly coloured at all stages of ripeness, and contrasted with the forest background (Table 1). In 25 Ficus taxa the figs darkened from an initial pre-mature green through orange to a tone of red or black, or through pink to purplish. In contrast, four species (F. caulocarpa, F. delosyce, F. sumatrana, F. virens) had dull figs, which did not undergo any significant colour changes upon ripening.

Avian fig-eating assemblages

During the study, 231 bird species were recorded within the study area, of which 60 species, representing 18 families, were recorded eating figs (Table 2). Fig-eating birds were found to include birds with diets ranging from almost entirely insectivorous (e.g. Diards Trogan *Harpactes diardii*) to entirely phytophagous (the pigeons; *Treron*, *Ptilinopus* and *Chalcophaps*).

Table 3 documents the assemblages of birds associated with 25 Ficus taxa with bird-eaten figs which were systematically watched during fruiting episodes. Due to the variation in the duration of observations from which these lists derive, the assemblages are not comparable. In order to overcome these problems of comparison, data are presented on bird visitation to a set of 15 Ficus species, each observed for 12 hours during the period of peak ripe fruit production (Table 4). In an attempt to reduce bias arising from the timing of observations, representative data from different times of the day were analysed. Similarly, bias derived from attributes of individual trees was reduced by using data from two trees wherever possible.

Green pigeons *Treron* spp. and barbets regularly ate figs of all sizes (Table 4). Since the green pigeons and *Megalaima* barbets comprise small groups of species which varied greatly in both body weight and gape size they were ideal taxa for investigating resource partitioning. Visitations to the 15 *Ficus* species by individual species within these two bird groups were therefore compared (Figures 1 and 2). Despite prolonged observations, forest-dwelling green pigeons were only seen to eat figs at the study site.

DISCUSSION

The size of bird-eaten figs at Kuala Lompat, ranging from the 4 mm diameter figs of F. sinuata to the 45.5×34.8 mm figs of F. subcordata span the whole size spectrum of bird-dispersed fruit at the study site. The colours exhibited by ripe figs at Kuala Lompat, with a predominance of red and purple tones, are

Table 2. Fig-eating bird species of Kuala Lompat. Birds recorded eating figs on greater than 50 occasions are marked with an asterisk. (Names follow King et al. 1975, except where more recent taxonomic revisions are quoted.) Bird species codes used in other tables are indicated.

	PHASIANIDAE	PM	*Pycnonotus melanoleucos. Black and White
LI	Lophura ignita. Crested Fireback.	. .	Bulbul.
		PA	*Pycnonotus atriceps. Black-headed Bulbul.
	COLUMBIDAE	PC	*Pycnonotus cyaniventris. Grey-bellied Bulbul.
TP	*Treron capellei. Large Green Pigeon.	\mathbf{PF}	Pycnonotus finlaysoni. Stripe-throated Bul
TC	*Treron curvirostra. Thick-billed Pigeon.		bul.
TF	Treron fulvicollis. Cinnamon-headed Pigeon.	PG	Pycnonotus goavier. Yellow-vented Bulbul.
TO	Treron olax. Little Green Pigeon.	PQ	†Pycnonotus squamatus. Scaly-breasted Bul
PJ	Ptilinopus jambu. Jambu Fruit-Dove.	nn	bul.
DB	Ducula badia. Mountain Imperial Pigeon.	PP	Pycnonotus plumosus. Olive-winged Bulbul.
CI	Chalcophaps indica. Green-winged Pigeon.	PS	*Pycnonotus simplex. Cream-vented Bulbul.
	DCITTA CIDA E	PB	*Pycnonotus brunneus. Red-eyed Bulbul.
T.C	PSITTACIDAE	\mathbf{PY}	*Pycnonotus erythropthalmos. Spectacled Bul
LG	Loriculus galgulus. Blue-crowned Hanging Parrot.	OT.	bul.
	rarrot.	CF	Criniger finschii. Finsch's Bulbul.
	TROGONIDAE	CB	*Criniger bres. Grey-cheeked Bulbul.
HD	Harpactes diardi. Diard's Trogon.	CP	*Criniger phaeocephalus. Yellow-bellied Bulbul.
ш	nurpuctes usurus. Diard's 110gon.	нс	*Hypsipetes criniger. Hairy-backed Bulbul.
	BUCEROTIDAE	НН	*Hypsipetes charlottae. Buff-vented Bulbul.
RV	*Rhinoplax vigil. Helmeted Hornbill.	HM	Hypsipetes malaccensis. Streaked Bulbul.
BR	*Buceros rhinoceros. Rhinoceros Hornbill.	HF	Hypsipetes flavala. Ashy Bulbul.
RC	Rhyticeros corrugatus. Wrinkled Hornbill.	111	Tryps: peres fuoum. Asiry Buildi.
AM			ORIOLIDAE
AA	Anthracoceros albirostris ¹ . Pied Hornbill.	OX	Oriolus xanthonotus. Dark-throated Oriole.
AG	*Anorrhinus galeritus. Bushy-crested Hornbill.	0.1	Sylvino Name Control Dalla Inicator Silvino
	, , , , , , , , , , , , , , , , , , , ,		CORVIDAE
	CAPITONIDAE	PL	Platysmurus leucopterus. Black Magpie.
MC	*Megalaima chrysopogon. Gold Whiskered Barbet.	CE	Corvus enca. Slender-billed Crow.
MM	*Megalaima mystacophanos. Red-throated Bar-		PARIDAE
	bet.	MS	Melanochlora sultanea. Sultan Tit.
MH	*Megalaima henricii. Yellow-crowned Barbet.		
MA	*Megalaima australis. Blue-eared Barbet.		TIMALIIDAE
CG	*Calorhamphus fuliginosus. Brown Barbet.	AB	*Alcippe brunneicauda. Brown Fulvetta.
			WIIDDID A E
	EURYLAIMIDAE	TO	TURDIDAE
CV	*Calyptomena viridis. Green Broadbill.	TO	Turdus obscurus. Eye-browed Thrush.
		ZI	Zoothera interpres. Chestnut-capped Thrush.
	CAMPEPHAGIDAE		CTUD NUD A E
CR	Coracina striata. Bar-bellied Cuckoo-Shrike.	CD	STURNIDAE
		GR	*Gracula religiosa. Hill Myna.
	CHLOROPSEIDAE		DICAEIDAE
CS	*Chloropsis sonnerati. Greater Green Leafbird.	FM	*Prionochilus maculatus. Yellow-breasted
CC	*Chloropsis cyanopogon. Lesser Green Leaf-		Flowerpecker.
	bird.	FP	*Prionochilus percussus. Crimson-breasted
CH	*Chloropsis cochinchinensis. Blue-winged Leaf-		Flowerpecker.
	bird.	FA	Dicaeum agile. Thick-billed Flowerpecker.
		FC	*Dicaeum chrysorrheum. Yellow-vented
	IRENIDAE ²		Flowerpecker.
IP	*Irene puella. Fairy Bluebird.	FT	Dicaeum trigonostigma. Orange-bellied Flowerpecker.
	PYCNONOTIDAE	FN	Dicaeum concolor. Plain Flowerpecker.
PZ	Pycnonotus zeylanicus. Straw-headed Bulbul.	FI	Dicaeum ignipectus. Buff-bellied Flower
	*Py cnonotus eutilotus. Puff-backed Bulbul.	• •	pecker.

¹ See Frith & Frith 1983. ² Inclusion of *I. puella* in Irenidae follows Campbell & Lack 1985.

[†] P. squamatus only observed eating figs at Taman Negara.

Table 3. Avian feedir eating the figs of 25 F birds coded as in Table	3. A the fi oded	igs of as in	feedi f 25 <i>I</i> Table	ng asse icus ta 2.	emblage axa. To	es of Fi	icus sp. ations	Table 3. Avian feeding assemblages of <i>Ficus</i> species of Kuala Lompat (and <i>F. virens</i> at Taman Negara). This table indicates which burd species were observed eating the figs of 25 <i>Ficus</i> taxa numbered according to Table 1; birds coded as in Table 2.	Kuala rvatio	Lom ns, in	pat (an hours,	d F. vi	rens a licated	t Tam I at th	e end	gara). of eac	This tach colu	ible me mn. Fi	ficates	xa nt	th birc	d acco	es were	o Tabl	e 1;
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TC	×	×	×	×		××	×	×	×		×	×		×	×			×	×	×	×	×	×	×	×
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MM	×		×	×	×	×		×	×		×	×	×	×	×		×	×		×	×	×	×		
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CG	×	×	×	×		×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×	×	
CV	×		×	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×		
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PA PC PF PG	PS PB	PQ CF TY	HHH	OX PL CE MS	AB TO ZI GR	FM FP FA	FT FN FI	

¹ F. virens: data derived from Taman Negara.

² Fallen fruit.

Table 4. Percentages of total avian visits by fig-eating bird taxa to 15 Ficus species. Each Ficus species was observed for a total of 12 hours. Total number of bird species in each taxon (N), and the range of mean weights (grams) and mean gapes (mm, determined from spirit specimens and live birds) within each taxon are indicated. Ficus species are arranged in order of increasing fruit size. Blank spaces indicate no visits; total number of visits to each Ficus species is indicated. Taxa as follows: GP-green pigeons (Treron spp.); BB-barbets; BU-bulbuls; FP-flowerpeckers; RP-Fairy Bluebird; CV-Green Broadbill; GR-Hill Myna; LB-leafbirds.

									Ficus t	аха (СD	Ficus taxa (CD: Table 1)	1)						
i				2	*4	5	∞	11	12	15	16	17	21	23	29	30	31	35
Bird taxon	(N)		Weight (g) Gape (mm)						Jo %)	total a	(% of total avian visits)	(5;						
HB	(4)	900-3100	43.6-61.0					5.2		1.8	9.1	9.1	3.2	7.6	18.7	2.4	6.8	11 5
GP	(3)	77-411	10.3 - 20.2	55.4	22.5	10.6	2.0	29.0	10.0	51.3	19.4			64.1	12.3	84.1	59.1	77.7
GR	Ξ	233	23.6	0.3	0.2			8.0	4.8	7.2	12.8			9.7	15.9			1.5
BB	(5)	27-156	15.0 - 26.2	7.3	59.6	5.2	16.0	32.4	30.9	10.3	14.5	19.8	36.7	24.8	19.0	12.9	16.4	4.6
Η	Ξ	62	14.0	1.5	8.9	3.9	3.2	11.8	6.9	3.2	6.1	14.9	11.5	3.8	26.3		1.8	
CV	(1)	57	21.7	0.1	2.5	3.9	2.1	2.3	0.4	1.9	4.2	15.7	5.1	9.0	9.0	0 1		
ΓB	(3)	23-43	9.8 - 13.1	3.6	4.6		2.0	7.3	5.7	4.6	4.3		2.8	2.5	5.1	0.1	9.0	8.0
BU	(12)	15-36	9.1 - 13.4	13.6	3.4	59.0	51.7	8.7	24.6	6.3	17.9	40.6	34.8	8.0	9.0		0.4	
FP	(4)	7-10	6.5-7.1	12.0	0.2	14.2	18.9	1.0	14.0	1.9	13.0			0.3			6.9	
Total r	umber	fotal number of visits		1227	503	310	661	523	461	822	572	121	312	1275	315	099	792	260

* F virens; data derived from Taman Negara; all other data from Kuala Lompat.

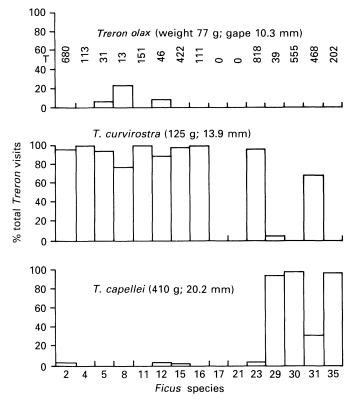


Figure 1. The percentage of total *Treron* pigeon visits to 15 *Ficus* species for three *Treron* species. Each *Ficus* species was observed for 12 hours. *Ficus* species are in order of increasing fruit size, and numbered according to Table 1. The total number of *Treron* visits to each *Ficus* species, T, is indicated in the top histogram.

typical of fruits which attract avian consumers (Corner 1949, Janson 1983, Knight & Siegfried 1983, Ridley 1930, Turcek 1963, van der Pijl 1969, Wheelwright et al. 1984, Willson & Thompson 1982), although these bright colours are also highly attractive to primates (Gautier-Hion et al. 1985, FRL pers. obs.).

However, 13.8% (four species) of the bird-dispersed *Ficus* taxa at Kuala. Lompat had dull-coloured ripe figs. In a comprehensive survey of bird-dispersed fruits in a Costa Rican forest, Wheelwright *et al.* (1984) found only six of 140 bird-dispersed species (4.2%) had brown or green fruits. Indeed, other studies have suggested that fleshy dull fruits (especially green coloured) are favoured by bats but avoided by birds (Fleming 1979), Gautier-Hion *et al.* 1985). August (1981) speculated that the absence of colour change by the ripening of the greenish figs of *F. trigonata* in Venezuela was an adaptation to dispersal by bats. In this study, however, there is no reason to believe that this was the case for species which remained dull on ripening.

At Kuala Lompat, the four *Ficus* species with dull-coloured figs attracted some of the largest concentrations of feeding birds recorded. It is possible that these trees rely on other traits to attract birds, such as huge crop size or high

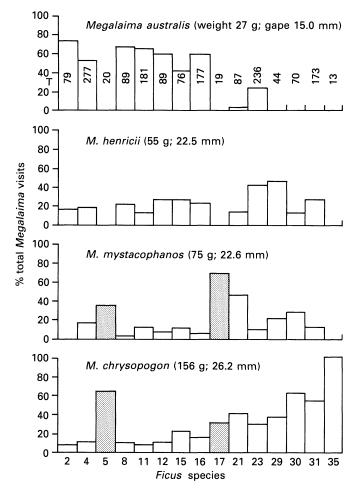


Figure 2. The percentage of total Megalaima pigeon visits to 15 Ficus species for three Megalaima species. Each Ficus species was observed for 12 hours. Ficus species are in order of increasing fruit size, and numbered according to Table 1. The total number of Megalaima visits to each Ficus species, T, is indicated in the top histogram. Shaded bars denote Ficus species growing in the understorey: this strata was rarely visited by M. australis or M. henricii.

nutritional rewards. All four species attain very large sizes, and produce enormous crops of small, densely packed figs (Lambert 1987).

The importance of figs to birds is reflected by the large proportion of the avifauna which consumed figs at Kuala Lompat. Although some species ate figs only rarely, other species (species of the groups in Table 4) regularly visited fruiting *Ficus* and consumed large quantities of figs. Indeed, this study has shown that green pigeons *Treron* spp. which inhabit forest are fig-eating specialists, although they are primarily seed predators (Lambert, in press.). Similarly, some barbets of the genus *Megalaima* are highly dependent on figs and may also be specialists, as suggested elsewhere (Lambert 1987, Leighton & Leighton 1983).

Although there was tremendous overlap in the sizes of figs consumed by

birds, irrespective of their body weight and gape size, some parameter of bird size appears to influence the sizes of fruits eaten by different bird species. This is reflected by the fairly distinct resource partitioning exhibited by both *Treron* pigeons and *Megalaima* barbets. Fig-size choice by other frugivorous bird groups also seems to be influenced by bird size (Table 4). During the twelve-hour observations at the 15 trees, larger birds (e.g. hornbills and Hill Myna *Gracula religiosa*) were proportionally much commoner visitors (despite their lower population densities) to larger-fruited *Ficus*, whilst small frugivorous species (e.g. bulbuls and flowerpeckers) tended to be commoner visitors to smaller-fruited *Ficus*. Thus, even though the succulent, fleshy nature of bird-eaten figs enables exploitation by birds of all sizes, the fig resource is partitioned by birds, albeit in a rather diffuse manner.

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LITERATURE CITED

- AUGUST, P. V. 1981. Fig fruit consumption and seed dispersal by Artibeus jamaicensis in the Llanos of Venezuela. Biotropica 13:70-76.
- BREITWISCH, R. 1983. Frugivores at a fruiting *Ficus* vine in a southern Cameroon tropical wet forest. *Biotropica* 15:125-128.
- BROCKELMAN, W. Y. 1982. Observations of animals feeding in a strangler fig F. drupacea in South-east Thailand. Natural History Bulletin of the Siam Society 30:33-44.
- CAMPBELL, B. & LACK, E. (eds). 1985. A dictionary of birds. T. and A. D. Poyser, Calton. 670 pp.
- CHIVERS, D. J. (ed.). 1980. Malayan forest primates. Plenum Press, New York. 388 pp.
- COATES-ESTRADA, R. & ESTRADA, A. 1986. Fruiting and frugivores at a strangling fig in the tropical rain forest of Los Tuxtlas, Mexico. Journal of Tropical Ecology 2:349-357.
- CORLETT, R. T. 1984. The phenology of Ficus benjamina and Ficus microcarpa in Singapore. Journal Singapore National Academy of Science 13:13.
- CORNER, E. J. H. 1949. The Durian theory or the origin of the modern tree. Annals of Botany 13:317-414.
- CORNER, E. J. H. 1965. Check list of *Ficus* in Asia and Australasia, with keys to identification. *Gardens' Bulletin Singapore* 21:1-186.
- FLEMING, T. H. 1979. Do tropical frugivores compete for food? American Zoologist 19:1157-1172.
- FRITH, C. B. & FRITH, D. W. 1983. A systematic review of the hornbill genus Anthracoceros (Aves, Bucerotidae). Zoological Journal of the Linnean Society 78:29-71.
- FROST, P. 1980. Fruit-frugivore interactions in a South African coastal dune forest. Proceedings XVII International Ornithological Congress Berlin.
- GAUTIER-HION, A., DUPLANTIER, J.-M., QUIRIS, R., FEER, F., SOURD, C., DECOUX, J.-P., DUBOST, G., EMMONS, L., ERARD, C., HECKETSWEILER, P., MOUNGAZI, A., ROUSSILHON, C. & THIOLLAY, J. M. 1985. Fruit characters as a basis of fruit choice and seed disposal in a tropical forest vertebrate community. *Oecologia* 65:324-337.
- HERRERA, C. M. 1981. Are tropical fruits more rewarding to dispersers than temperate ones? American Naturalist 118:896-907.

- JANSON, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a tropical forest. Science 219: 187-189.
- JANZEN, D. H. 1980. How to be a fig. Annual Review Ecology & Systematics 10:13-51.
- JOHNS, A. D. 1983. Ecological effects of selective logging in a West Malaysian rain forest. Unpublished PhD thesis, Cambridge University.
- JORDANO, P. 1983. Fig-seed predation and dispersal by birds. Biotropica 15:38-41.
- KANTAK, G. E. 1979. Observation on some fruit eating birds in Mexico. Auk 96:183-186.
- KING, B., WOODCOCK, M. & DICKINSON, E. C. 1975. A field guide to the birds of South-east Asia. Collins, London. 480 pp.
- KNIGHT, R. S. & SIEGFRIED, W. R. 1983. Inter-relationships between type, size and colour of fruits and dispersal in Southern African trees. *Oecologia* 56:405-512.
- LAMBERT, F. R. 1987. Fig-eating and seed dispersal by birds in a Malaysian lowland rain forest. Unpublished PhD thesis, University of Aberdeen.
- LAMBERT, F. R. in press. Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. Ibis.
- LEIGHTON, M. 1982. Fruit resources and patterns of feeding, spacing and grouping among sympatric Bornean hornbills (Bucerotidae). Unpublished PhD thesis, University of California, Davis.
- LEIGHTON, M. in press. Phenological patterns in Asian rain forest communities. Proceedings of the International Workshop on Reproductive Ecology of Tropical Forest Plants, UNESCO(MAB), IUBS. Bangi, Malaysia 1987.
- LEIGHTON, M. & LEIGHTON, D. R. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pp. 181-196 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. Tropical rain forests: ecology and management. Blackwell Scientific Publications, Oxford.
- McCLURE, H. E. 1966. Flowering, fruiting and animals in the canopy of a tropical rain forest. *Malayan Forester* 24:182-203.
- MEDWAY, LORD. 1972. Phenology of a tropical rainforest in Malaya. Biological Journal of the Linnean Society London 4:117-146.
- MEDWAY, LORD & WELLS, D. R. 1971. Diversity and density of birds and mammals at Kuala Lompat, Pahang. *Malayan Nature Journal* 4:238-247.
- MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit-eating in tropical birds. American Naturalist 107:8-22.
- NG, F. S. P. (ed.). 1978. Tree flora of Malaya. Vol. 3. Longman, Kuala Lumpur. 339 pp.
- PIJL, L. VAN DER 1969. Principles of dispersal in higher plants. Springer-Verlag, New York. 154 pp.
- PRATT, T. K. 1983. Seed dispersal in a montane forest in Papua New Guinea. Unpublished PhD thesis, Rutgers University, New Jersey.
- PRATT, T. K. & STILES, E. W. 1985. The influence of fruit size and structure on composition of frugivore assemblages in New Guinea. *Biotropica* 17:314-372.
- RAEMAEKERS, J. J., ALDRICH-BLAKE, F. P. G. & PAYNE, J. B. 1980. The forest. Pp. 29-61 in Chivers, D. J. (ed.). Malayan forest primates. Plenum Press, New York.
- RIDLEY, H. N. 1930. The dispersal of plants throughout the world. L. Reeve & Co., Kent, England. 744 pp.
- SCOTT, P. E. & MARTIN, R. F. 1984. Avian consumers of Bursera, Ficus and Ehretia fruits in Yucatan. Biotropica 16:319-323.
- SNOW, B. K. & SNOW, D. W. 1971. The feeding ecology of tanagers and honey creepers in Trinidad. Auk 291-322.
- SNOW, D. W. 1980. Regional differences between tropical floras and the evolution of frugivory. *Proceedings XVII International Ornithological Congress*. Pp. 1192-1198.
- TERBORGH, J. 1986. Keystone plant resources in the tropical forest. In Soule, M. E. (ed.). Conservation biology, the science of scarcity and diversity. Sinauer Associates Inc., Massachussets. 584 pp.
- TERBORGH, J. & DIAMOND, J. M. 1970. Niche overlap in feeding assemblages of New Guinea birds. Wilson Bulletin 82:29-52.
- TURCEK, F. J. 1963. Colour preferences in fruit and seed-eating birds. *Proceedings XIII International Ornithological Congress* 1962. Ithaca, New York, Pp. 285-92.
- WELLS, D. R. 1975. Bird report: 1972 and 1973. Malayan Nature Journal 28:186-213.
- WELLS, D. R. 1982. Bird report: 1974 and 1975. Malayan Nature Journal 36:61-85.
- WHEELWRIGHT, N. T., HABER, W. A., MURRAY, K. G. & GUINDON, C. 1984. Tropical fruit eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16:173–192.
- WHITE, S. C. 1974. Ecological aspects of growth and nutrition in tropical forest fruit eating birds. Unpublished PhD thesis, University of Pennsylvania.
- WILLSON, M. F. & THOMPSON, J. N. 1982. Phenology and ecology of color in bird dispersed fruits or why some fruits are red when they are 'green'. Canadian Journal of Botany 60:701-713.

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