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KEYSTONE CHARACTERISTICS OF BIRD-DISPERSED *FICUS* IN A MALAYSIAN LOWLAND RAIN FOREST

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SUMMARY

(1) The fruiting of 307 *Ficus* trees in 74 ha of lowland forest at Kuala Lompat, Malaysia, was monitored monthly for 3 years.

(2) The guild of twenty-nine species of bird-dispersed *Ficus* exhibited asynchronous fruiting phenology, with no recurrent annual pattern. Fig crops were available in all 36 months of the study, but whilst medium-sized and small-sized figs were always available, crops of large-fruited (mean fig diameter of > 20 mm) bird-dispersed *Ficus* were scarce, with only around sixteen fruiting events year^{-1} km^{-2} of forest.

(3) Seven *Ficus* species exhibited fruiting patterns which suggested some seasonality, with significantly more fruitings than expected in the period February–April. This period is before the usual major annual community peak in fruiting, at a time when other fruit resources are relatively scarce.

(4) *Ficus* forms a uniquely important group within the subset of plants with bird-eaten fruit because of their numerical abundance, intra-crown synchrony of fruit ripening, relatively short intervals between fruiting, large crop sizes and intra-population fruiting asynchrony. These characteristics, combined with their availability at times when other fruits are scarce, makes *Ficus* a most important keystone plant resource.

(5) For frugivores to be dependent on figs in South-east Asia they need to be wide-ranging. Frugivorous birds with small home ranges may have to rely on keystone plants other than *Ficus* during some periods of fruit scarcity.

INTRODUCTION

Studies of avian frugivory in the tropics have led to the concept of pivotal plant species (Howe 1977) and keystone plant resources (Terborgh 1986a). These plants perform a critical function in the forest ecosystem because they sustain frugivorous animal species and communities through periods of resource scarcity. For frugivores, keystone plant taxa are those that produce fruit during periods when other fruit resources are insufficient to meet frugivore nutritional requirements. Present evidence suggests that, at any one location, a number of plant genera or species may act as keystone taxa (Terborgh 1986b, Leighton & Leighton 1983). Each of these taxa provides fruit during periods of general scarcity, but not necessarily simultaneously.

Deletions of keystone plant species or species groups would potentially result in the extinction of frugivores which depend on them during periods of resource scarcity. Such extinctions could have further repercussions for the ecosystem, such as the eventual loss of other plants which were dependent on seed dispersal by these frugivorous species. Such a scenario obviously has serious implications for forest management and conservation.

In Peru (Terborgh 1986b) and Borneo (Leighton & Leighton 1983) *Ficus* species constitute probably the most important group of keystone plant resources. This may also be true in Panama (Foster 1982, Windsor *et al.* 1989), but in a Gabon rain forest fruiting *Ficus* occur at such low densities that they do not act as keystone plant resources for the majority of frugivorous animals (Gautier-Hion & Michaloud 1989). Nevertheless, circumstantial evidence suggests that *Ficus* may play a more important role in sustaining frugivores in other African rain forests (Gautier-Hion & Michaloud 1989).

Despite the accepted doctrine that *Ficus* species are of exceptional importance to forest frugivores, no studies have looked in detail at the fruiting characteristics that underline this importance. This paper investigates the keystone status of *Ficus* by examining the traits which contribute to the unique role that *Ficus* plays in providing birds with a year round supply of carbohydrate-rich fruit (figs) in a Malaysian lowland forest.

Malaysian forests are extremely rich in *Ficus* species, with about 16% (101) of known world species (Ng 1978). The density of *Ficus* is reported to be of the order of two to three trees per hectare at two West Malaysian lowland forest sites (Johns 1983, Lambert 1987), and thirty-eight species were found in 2 km^2 at one of these (Kuala Lompat: Lambert 1989a). At least sixty species of bird and seventeen species of mammal eat figs in Peninsular Malaysian lowland forests (Lambert 1989b, 1990).

STUDY AREA AND METHODS

The study site, 210 ha of lowland (50–80 m a.s.l.) Evergreen Dipterocarp Forest at Kuala Lompat (3°43′N, 102°17′E), Peninsular Malaysia, is described in detail elsewhere (Raemaekers, Aldrich-Blake & Payne 1980; Lambert 1987, 1989a, 1989c).

Ficus plants within 20 m of trails in 95 ha of the study site were labelled and mapped during early 1984. Although it is unlikely that all small individuals in this area were found, all *Ficus* large enough to be of importance to frugivorous birds were thought to have been located. The resulting transects sampled 74 ha of the study site. Voucher specimens of leaves and fruits were used to identify *Ficus* species by comparison with labelled herbaria material. These specimens were deposited in herbaria at the Royal Botanic Gardens, Kew, and at the University of Malaya, Kuala Lumpur. Fruitings of *Ficus* in the sample (which varied from 244 to 307 trees because new plants were added to the sample during the first 6 months, whilst forty-eight died during the study) were monitored at the beginning of each month from March 1984 until May 1987. Surveys were carried out during as few consecutive days as possible (usually three days) in order to obtain an ‘instantaneous’ picture of fruiting. When present, figs were scored as either young, unripe or ripe.

In this paper only crops of ripe figs are considered, and only those of species dispersed by birds. Fruits of nine *Ficus* species identified at Kuala Lompat were never, or extremely rarely, consumed by birds (Lambert 1989a), and are therefore not considered as bird-dispersed species. Ripe bird-dispersed figs were soft and fleshy, usually contained seeds but never latex, and were invariably found on the ground below the tree, often in large numbers. Mean fig size was calculated from measurements of intact, fresh, ripe figs collected from two or three trees, with the exception of *F. subulata*, *F. trichocarpa* and *F. binnendykii*, for which only one tree was sampled. These were collected from the ground, or if possible, directly from the tree. As most fallen figs were damaged, sample sizes were mostly small.

It was not possible to collect data systematically from July to mid-October 1985. During this period a local field assistant collected all phenological data, but because it was not certain exactly when some *Ficus* fruited during this period some data have been lumped. During this period the gaps between collections were sometimes greater than 1 month. As a consequence it is possible that fruiting by species with short pre-ripening display and crop persistence (*Ficus obscura* and *F. heteropleura*) were missed.

Not all *Ficus* fruited: those that did not were mostly of immature size, and these are not considered in subsequent discussion. A few non-fruiting trees were of mature size, defined as the minimum size, estimated as crown volume, which fruited during the study. Crown volume was estimated from the ground from measurements of its average horizontal dimension along two perpendicular lines and an estimate of crown depth. In cases where the crown was patchily distributed, volume estimations took this into account. Because there is undoubtedly error in making such estimations, each crown was allocated to one of six size categories based on the linear dimension of a cube (Lambert 1987) (Table 2).

Ficus crop persistence, defined as the period from the time that figs first ripened until the crop had been completely depleted by frugivores (at this stage fewer than 1% of the fruit remained but no frugivore visitors), was recorded whenever possible. Crop size was estimated by counting figs in one small part of a tree, and then multiplying by the total number of such small parts. Dates of fruiting were used to calculate fruiting intervals (the time between sequential ripe crops of individual *Ficus*), but it must be noted that these calculations take no account of trees of apparently mature size which did not fruit during the study. Fruiting-interval calculations did not include the period July–October 1985 unless it was certain that there was no possibility of a missed fruiting event.

RESULTS

Sizes of mature bird-dispersed Ficus *trees*

The species of bird-dispersed *Ficus* at Kuala Lompat are shown in Table 1. The mature size of *Ficus* plants varied between species; whilst species such as *F. subulata*, *F. virens* and *F. heteropleura* fruited when they were small, with crown volume less than 8 m^3, other species, such as *F. caulocarpa* and *F. delosyce*, did not fruit until their canopy volume reached 512–4096 m^3. However, most species (twenty-two of the twenty-nine species represented in the sample by individuals of various sizes) were capable of producing fruit when canopy volume reached *c.* 64 m^3 (Table 2). All five species with large figs (> 20 mm in mean diameter) were exceptional in that they never fruited until they had reached *c.* 216–512 m^3.

Crop persistence and crop size

Crops of bird-dispersed figs took 3–12 weeks to develop (although 12 weeks was exceptional), and during this period were displayed in their unripe colours (Table 3). All species showed some variation in the length of pre-ripening display time. There

TABLE 1. Bird-dispersed *Ficus* species of Kuala Lompat. Taxonomy and order follow Corner (1965). *n* is the number of individuals of each species in the phenological sample.

Ficus species	*n*
Subgenus *Urostigma* (monoecious)	
F. benjamina L.	11
F. binnendykii Miq.	8
F. bracteata Wall. ex King	7
F. caulocarpa Miq.	17
F. consociata Bl. (var. *murtoni* King)	11
F. crassiramea Miq.	6
F. cucurbitina King	10
F. delosyce Corner	5–6†
F. drupacea Thunb.	1
F. dubia Wall. ex King	1
F. kerkhovenii Val.	7
F. pellucido-punctata Griff.	16–17†
F. pisocarpa Bl.	9
F. stricta Miq.	1
F. stupenda Miq.	20
F. subcordata Bl.	3
F. sumatrana Miq.	5–6†
F. sundaica Bl. (three taxa)*	9; 8–9; 6–7†
F. virens Ait. (var. *glabella* (Bl.) Corner)	8
Subgenus *Ficus* (dioecious)	
F. heteropleura Bl.	8–9†
F. obscura Bl. (var. *borneensis* (Miq.) Corner)	23
F. parietalis Bl.	15
F. recurva Bl.	1
F. sagittata Vahl	3
F. trichocarpa Bl.	9
F. sinuata Thunb.	1
F. subulata Bl.	4

* Three distinct taxa, treated as species; see Lambert (1987) for a description.

† Identification of one (immature) individual uncertain.

was some variation between individuals of the same species in crop persistence, so that values presented in Table 3 are not necessarily typical for the whole population.

Individual trees of four bird-dispersed *Ficus* species (17·4% of the species) had crops which sometimes persisted for 18 days or longer, whilst individuals of seventeen species (74%) had crops which usually lasted for 14 days or less. Nine of the latter (39%) were completely depleted in 7 days or less on at least one occasion. The majority of bird-dispersed *Ficus* therefore usually produced fruit crops which ripened and were depleted by frugivores within 1 or 2 weeks. Most crop sizes were large, but making realistic estimates of the number of fruits was often impossible from the ground. Estimates, which were considered to be fairly accurate, were mostly therefore made from the canopy (Table 2).

Whilst most fruitings of *Ficus* involved fruit production in 80–100% of the crown, much smaller crops, here termed 'minor fruitings', were also regularly recorded. Minor fruitings were those that were considered to be of minor importance to frugivorous birds, involving less than 40% of the crown in the case of *Ficus* with crowns of less than *c.* 64 m^3 volume; less than 20% for crowns of 64–512 m^3; and less than 10% for crowns exceeding this volume.

TABLE 2. Estimated crop and crown sizes, and mean fig diameters of bird-dispersed *Ficus*. Crop size estimates are for one fruiting by one tree of each species. Crown size is expressed as the linear dimensions of a cube (m) (< 1 tiny, 1–2 small, 2–4 medium, 4–8 large, 8–16 very large, > 16 huge). Mean fig diameter is given as length × width (mm); *n* = number of figs measured.

Ficus species	Crop size (*n*)	Crown size	Mean fig diameter (mm)	*n*
F. subulata	300	1–2	10·4 × 10·4	4
F. obscura	4000	1–2	7·1 × 7·8	19
F. heteropleura	4500	1–2	7·6 × 7·7	8
F. sagittata	1000	2–4	12·0 × 12·0	30
F. trichocarpa	2600	2–4	15·5 × 17·5	8
F. obscura	7500	2–4	7·1 × 7·8	19
F. pisocarpa	12 000	4–8	11·6 × 12·3	21
F. pellucido-punctata	3000	4–8	17·7 × 11·6	15
F. stupenda	7500	4–8	32·4 × 27·4	17
F. binnendykii	10 000	4–8	8·5 × 7·8	8
F. pellucido-punctata	19 000	8–16	17·7 × 11·6	
F. cucurbitina	21 000	8–16	30·9 × 20·3	14
F. delosyce	50 000	8–16	10·1 × 11·0	34
F. dubia	4000	> 16	28·6 × 27·6	10
F. subcordata	5000	> 16	45·5 × 34·8	18
F. sundaica (taxon 1)	27 500	> 16	16·6 × 16·8	17
F. kerkhovenii	45 000	> 16	13·3 × 11·9	85
F. caulocarpa	250 000	> 16	5·4 × 5·9	39

TABLE 3. Duration of pre-ripening crop display and the persistence of the ripe crop of bird-dispersed *Ficus* at Kuala Lompat.

Ficus species	Display (weeks)	Persistence (days)	*n*
*F. obscura**	3–4	5–14	7
*F. parietalis**	4–5	5	1
F. sundaica (taxon 2a)	4–6	5	7
F. kerkhovenii	5	6– < 12	2
F. drupacea	4–5	7	1
F. cucurbitina	4	7–8	2
*F. heteropleura**	3–4	7–11	4
F. pisocarpa	4–6	7– < 12	5
F. stupenda	7–12	7–13	4
F. sundaica (taxon 2b)	4–7	8– < 18	4
F. binnendykii	4–5	< 9	2
F. dubia	4–5	9	1
F. pellucido-punctata	5–7	< 10	3
F. benjamina	3–4	< 11	1
F. consociata	6	12	2
*F. subulata**	4	> 12	1
F. sumatrana	3–4	< 14	1
F. delosyce	3–7	< 14	2
F. crassiramea	5–9	14– > 30	3
F. bracteata	8–9	< 17	2
F. sundaica (taxon 1)	4–8	< 18	2
F. stricta	4–6	> 18	1
*F. trichocarpa**	7–10	55–60	2

* Values for seed fig crops (figs of female plants of dioecious species).

Of the forty-nine minor fruitings recorded for bird-dispersed *Ficus* species, twenty-two involved less than 5% of the fruiting crown, and of these, ten involved less than 1%. Minor fruitings were recorded for individuals of 55% of bird-dispersed species at Kuala Lompat (see Fig. 3).

Fruiting phenology

At Kuala Lompat there were 427 fruitings by 126 bird-dispersed *Ficus* of twenty-nine species during 36 months. Forty-six *Ficus* of mature size did not fruit during this period, whilst other *Ficus* in the original sample of between 244 and 307 were either not bird-dispersed or immature. Bird-dispersed *Ficus* were available in every month (Fig. 1). Excluding minor fruitings ($n = 49$), the proportion of mature bird-dispersed *Ficus* which bore ripe fruit per month varied between 1·4% and 16·8% of the phenological sample, with a mean value of 6·4 ± 2·8% ($n = 32$ months). If minor fruitings are included, this proportion varied from 1·4% to 20·3%, with a mean of 10·5 ± 4·81. There were no distinct patterns of fruitings (Fig. 1), and no significant correlations between fruiting and monthly rainfall, rainfall 1 month before, 2 months

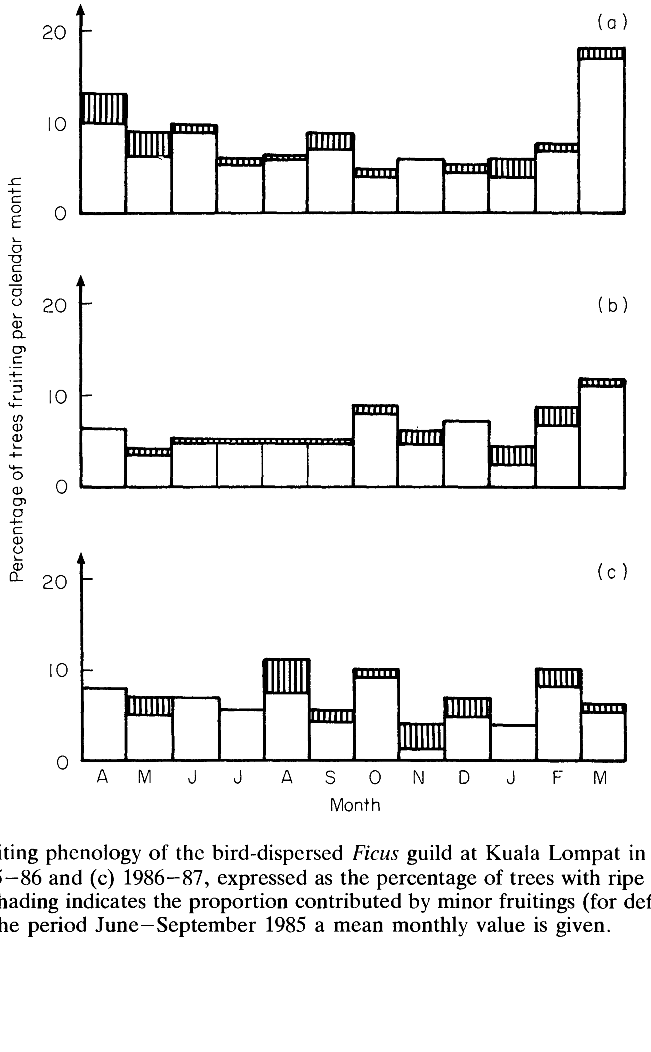


FIG. 1. Fruiting phenology of the bird-dispersed *Ficus* guild at Kuala Lompat in (a) 1984–85, (b) 1985–86 and (c) 1986–87, expressed as the percentage of trees with ripe fruit crops month^{-1}. Shading indicates the proportion contributed by minor fruitings (for definition see text). For the period June–September 1985 a mean monthly value is given.

before or 3 months before (Lambert 1987). Minor fruitings were not correlated to non-minor fruitings ($r = -0{\cdot}02$, $n = 32$, $P > 0{\cdot}05$). However, the number of *Ficus* trees with large figs (>20 mm mean diameter) which fruited per month was correlated with the number of medium-fruited (12–20 mm mean fig diameter) *Ficus* tree fruitings per month ($r = 0{\cdot}47$, $n = 33$, $P < 0{\cdot}05$), and the number of *Ficus* trees with medium-sized figs fruiting per month was correlated with the number of fruitings by small-fruited (<12 mm mean fig diameter) *Ficus* ($r = 0{\cdot}46$, $n = 34$, $P < 0{\cdot}01$) (see Fig. 2). This would suggest that perhaps all *Ficus* species respond to the same (unknown) fruiting cues.

Although bird-dispersed figs were available in every month, large figs (>20 mm mean diameter) were in scarce supply at the study site. Within the 74-ha phenological sample area there were never more than three (non-minor) fruitings of large-fruited *Ficus* per month, and in 14 of 36 months there were no such fruitings (Fig. 2). Indeed, during the 8-month period May 1985–December 1985, there were only two fruitings of trees with large bird-dispersed figs (although a *F. stupenda* just outside the phenological plot produced fruit in June or July 1985).

In total there were five species of *Ficus* that provided large bird-dispersed figs within the study area: *Ficus cucurbitina*, *F. drupacea*, *F. dubia*, *F. stupenda* and *F. subcordata*. Of twenty-seven individual trees of mature size, only sixteen fruited during the thirty-six-month period, producing a total of thirty-six fruitings. There

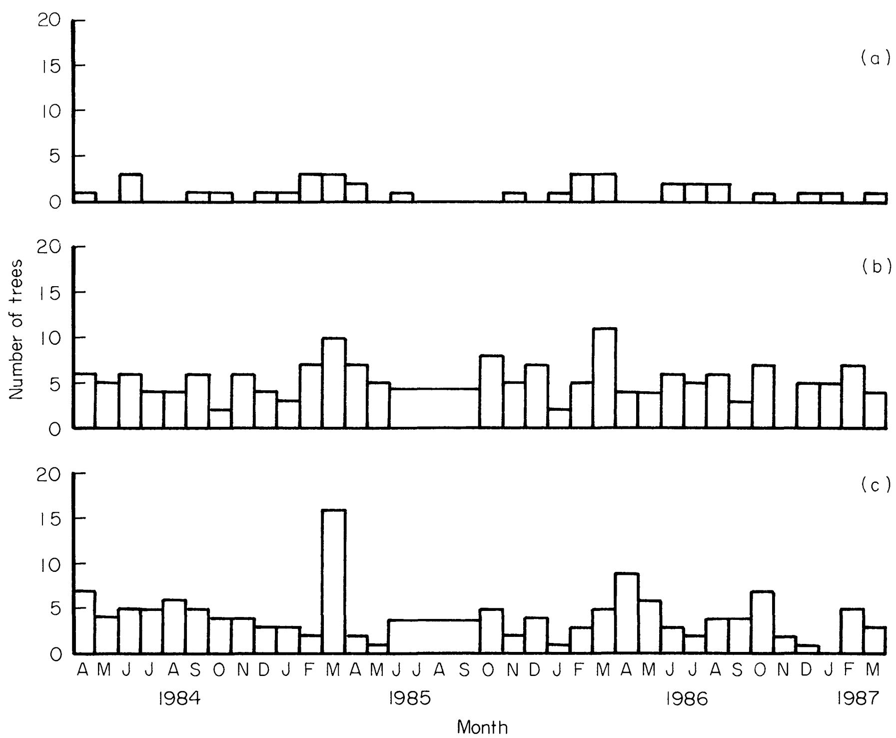


FIG. 2. The availability of bird-dispersed figs of (a) large-fruited species (mean fig diameter >20 mm), (b) medium-fruited species (12–20 mm) and (c) small fruited species (<12 mm) at Kuala Lompat expressed as the number of trees bearing ripe figs month^{-1} (minor fruitings excluded). For the period June–September 1985 a mean monthly value is given for medium- and small-fruited species.

TABLE 4. Fruiting intervals in months of bird-dispersed *Ficus* species at Kuala Lompat. Values are means ± 1 S.D. Fruiting interval is the time between the end of one fruiting and the beginning of the next.

Ficus species	Mean fruiting interval	*n*	Range
Small-fruited species (< 12 mm in diameter)			
F. benjamina	8·5 ± 2·4	4	5–10
F. binnendykii	14·8 ± 6·4	9	10–30
F. caulocarpa	12·3 ± 4·0	6	8–19
F. delosyce	4·2 ± 1·7	37	1–8
F. heteropleura	9	1	
F. obscura	6·3 ± 2·6	17	4–12
F. recurva	> 33	1	
F. sagittata	11·2 ± 6·1	6	6– > 20
F. sinuata	5·0 ± 2·6	7	2– > 10
F. subulata	> 22	1	
F. sumatrana	8·9 ± 7·5	7	3–24
F. virens	13·5 ± 0·7	2	13,14
Medium-fruited species (12–20 mm in diameter)			
F. bracteata	12·8 ± 3·3	6	7–16
F. consociata	7·9 ± 3·0	24	2–13
F. crassiramea	7·2 ± 1·3	9	5–9
F. kerkhovenii	6·7 ± 2·3	9	3–9
F. parietalis	18·0	2	17,19
F. pellucido-punctata	11·1 ± 5·8	18	4–29
F. pisocarpa	10·0 ± 2·2	9	6–13
F. stricta	8·0 ± 3·7	4	4–13
F. sundaica (taxon 1)	6·1 ± 2·9	31	3–14
F. sundaica (taxon 2a)	8·0 ± 3·5	24	3–18
F. sundaica (taxon 2b)	7·1 ± 1·5	22	6–10
F. trichocarpa	10·3 ± 3·6	6	6–17
Large-fruited species (> 20 mm in diameter)			
F. cucurbitina	19·5 ± 6·1	4	12– > 35
F. drupaceae	25	1	
F. dubia	14·0 ± 4·2	2	11,17
F. stupenda	11·1 ± 2·0	12	8–13
F. subcordata	13·5 ± 2·1	2	12,15

was a mean of twelve fruiting events year^{-1} in 74 ha of forest, suggesting only around sixteen fruitings by large-fruited bird-dispersed *Ficus* km^{-2} year^{-1}. In contrast, there were sixty-two fruitings by medium-fruited *Ficus* year^{-1} in 74 ha (*c.* 84 km^{-2} year^{-1}) and approximately forty-nine by small-fruited *Ficus* (*c.* 67 km^{-2} year^{-1}).

Medium-fruited and small-fruited *Ficus* crops were both available in all but 2 months (Fig. 2). There were at least three medium-fruited individuals producing ripe fruit crops in all but 3 months, and fruit production by these species was relatively even throughout the period of data collection, with a mean of 5·3 ± 2·2 ($n = 32$ months) fruitings month^{-1}. In contrast, small-fruited *Ficus* crops were often scarcer, with two or less trees producing ripe crops in 9 of 36 months, and fruiting was less even; the mean number of ripe fruitings month^{-1} was 4·2 ± 2·9 ($n = 32$ months).

A comparison of fruiting intervals (Table 4) showed that median values for large-fruited *Ficus* species were significantly longer than median values for species with medium-sized fruits (Mann–Whitney *U*-test; $U = 4{\cdot}5$, $P < 0{\cdot}05$) and species with small fruits ($U = 6{\cdot}5$, $P < 0{\cdot}05$). *Ficus stupenda* was exceptional, with a mean fruiting interval of less than 1 year; some individuals occasionally produced fruits at intervals of only 8 months. All other large-fruited bird-dispersed *Ficus* had supra-annual mean fruiting intervals. It must be noted, however, that the calculation of fruiting intervals does not take into account those *Ficus* which had apparently reached a size where they could fruit (judged from conspecifics) but did not do so during the study. Mean fruiting intervals may therefore be underestimated for some species. For all species, fruiting intervals were highly variable, even for individual trees.

Fruiting by individual species

The fruiting phenology of individual species of *Ficus* at Kuala Lompat is shown in Fig. 3. Although the sample size for the majority of species is small, the overall picture was one of aseasonality, with little evidence of intraspecific synchrony in fruiting. There were no correlations between the rainfall pattern and incidence of fruiting at the species level (Lambert 1987).

Nevertheless, a few species did exhibit fruiting patterns which suggested some seasonality in fruiting, mostly with a tendency to fruit in the period February to April. For seven species, there were significantly more fruitings than expected in these months: *F. benjamina* ($t = 3{\cdot}07$, $P < 0{\cdot}01$), *F. binnendykii* ($t = 7{\cdot}48$, $P < 0{\cdot}01$), *F. caulocarpa* ($t = 2{\cdot}73$, $P < 0{\cdot}05$), *F. consociata* ($t = 3{\cdot}66$, $P < 0{\cdot}01$), *F. pellucido-punctata* ($t = 2{\cdot}67$, $P < 0{\cdot}05$), *F. stupenda* ($t = 5{\cdot}88$, $P < 0{\cdot}01$), *F. sundaica* taxa 1 ($t = 3{\cdot}32$, $P < 0{\cdot}01$).

Although *F. crassiramea* was represented by only two trees which fruited, both fruited at regular intervals of 5–7 months (Fig. 3) and within 6 weeks of each other in all instances of fruiting. The single individuals of two large-fruited species, *F. subcordata* and *F. dubia*, which bore fruit, did so almost synchronously despite variations in fruiting intervals.

DISCUSSION

Bird and non-bird dispersed figs: a comparison

Whilst this study has identified species of *Ficus* important and unimportant to birds in Malaysian lowland forest (see also Lambert 1989a), the principal dispersal agents of *Ficus* that are not bird-dispersed are poorly documented. Table 5 provides a summary of known information on fruiting characteristics of non-bird dispersed species, derived largely from this study (Lambert 1987). Figs of non-bird-dispersed species differ from those of bird dispersed species in that they tend to be larger, duller coloured, less fleshy when ripe and are often displayed in places (such as against the main host tree trunk) awkward for harvesting by birds (Lambert 1987, 1989a). Table 5 suggests that species that are not bird-dispersed also usually differ from bird-dispersed species in at least one fruiting characteristic.

The vines, *F. aurantiacea*, *F. punctata* and *F. ruginervia*, produce very large figs adjacent to the trunks and larger branches of canopy trees, and have very small fig crops which persist for a relatively long time when compared to those of bird-dispersed *Ficus*. As a consequence, only a few figs are ripe at any one time, although crops are produced at very short intervals. The caulocarpous bat- or arboreal-mammal-

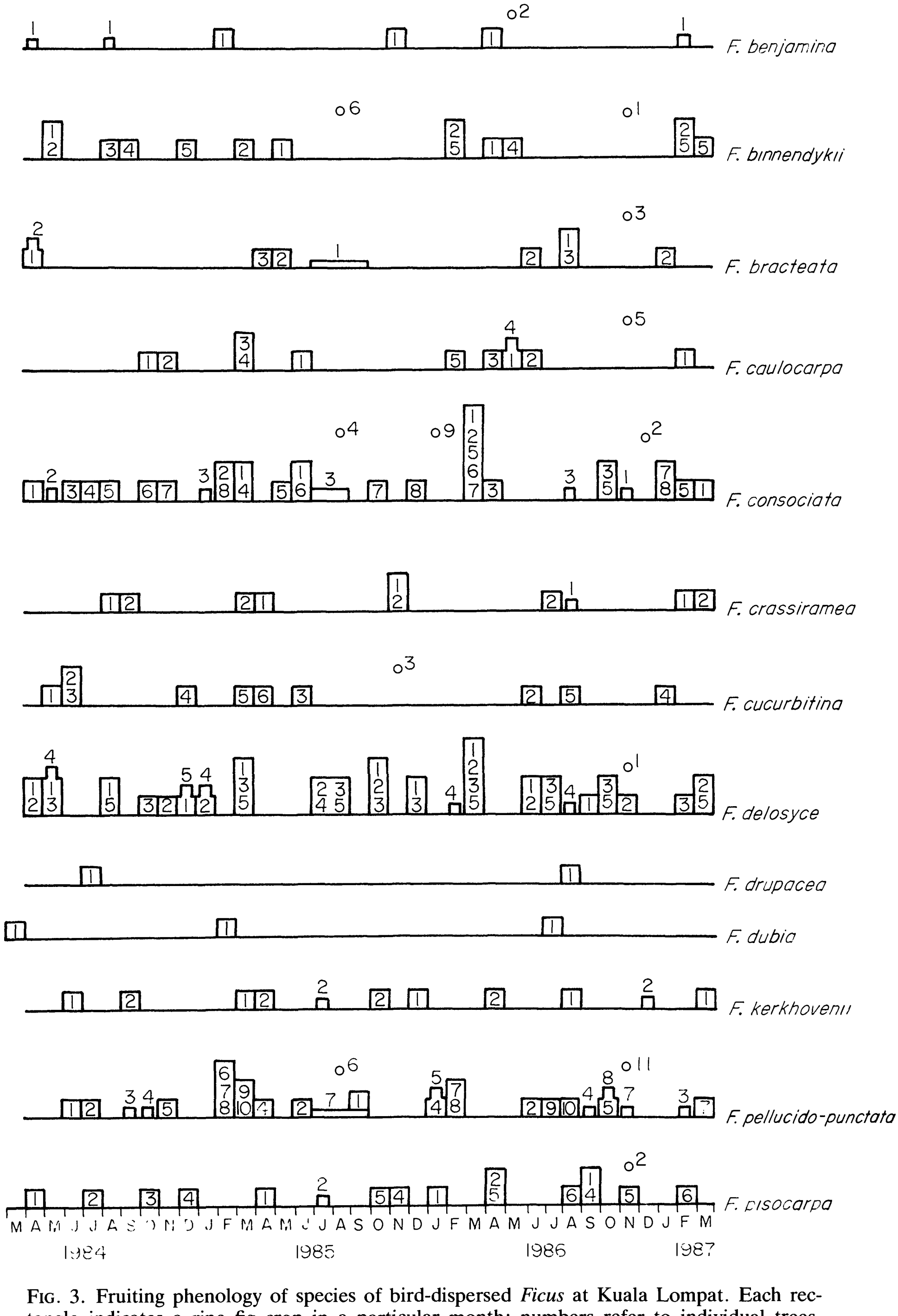
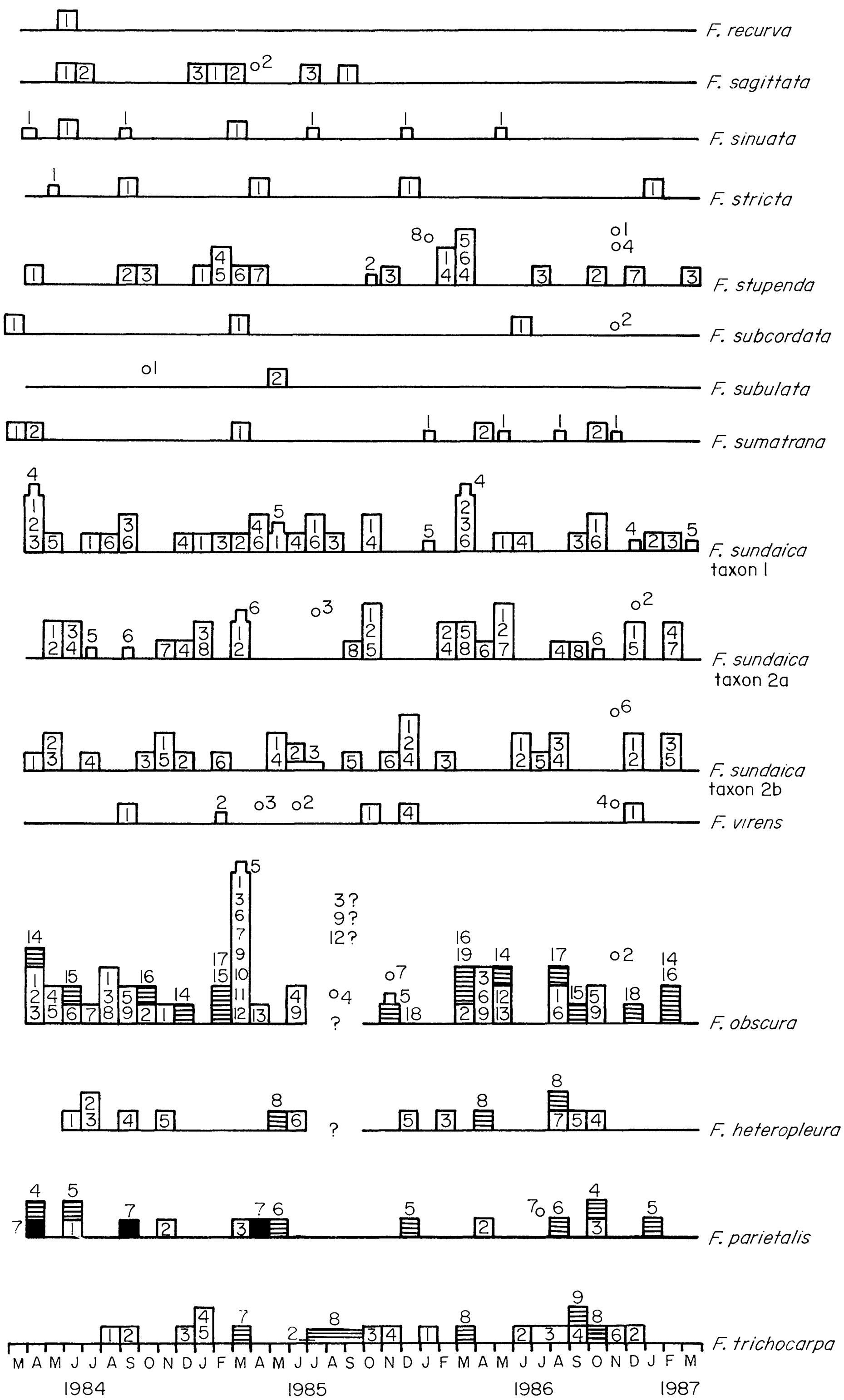


FIG. 3. Fruiting phenology of species of bird-dispersed *Ficus* at Kuala Lompat. Each rectangle indicates a ripe fig crop in a particular month: numbers refer to individual trees. Small rectangles indicate minor fruitings. Tree death is indicated by a circle. Rectangles extending over more than 1 month in the period June–September 1985 indicate where the exact timing of fruiting was not determined: mean number of fruitings month^{-1} are given in these instances.


F. recurva
F. sagittata
F. sinuata
F. stricta
F. stupenda
F. subcordata
F. subulata
F. sumatrana
F. sundaica taxon 1
F. sundaica taxon 2a
F. sundaica taxon 2b
F. virens
F. obscura
F. heteropleura
F. parietalis
F. trichocarpa
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1986
1987

TABLE 5. Some non-bird-dispersed *Ficus* spp. of Malaysia lowland forests: growth form, dispersal agents and fruiting characteristics (fruiting-interval data given are means ± 1 S.D. with ranges in parentheses). Data from Lambert (1987) unless stated otherwise.

Ficus species	Growth form‡	Dispersal agents§	Mean fig size (mm)	Typical crop size	Crop persistence (days)	Fruiting interval (months)
F. ruginervia Corner*	V	A,T,H	'golf ball'	?	45	6·8 ± 2·2 (3–12)
F. aurantiacea Griff.	V	A,T,H?	70	1–100	>30	0
F. punctata Thunb.	V	A,T	70	12–25	50	5·2 ± 1·5 (3–7)
F. depressa Bl.	SE	B,A,T?	32·7	1000–3000	10–14	11·9 ± 3·1 (7–18)
F. annulata Bl.	SE	B,A,T?	?	100–1000	14	12·7 ± 3·6 (9–24)
F. variegata Bl.	T	B,T,A?	?	> 5000	?	5·6 ± 3·1 (2–11)
F. fistulosa Reinw. ex Blum†	T	B,T	?	?	?	2·5 (2–3)

* Data from Medway (1972), † Data from Corlett (1987).
‡ V = vine; SE = scrambling epiphyte; T = tree.
§ Known dispersal agents: A = arboreal mammals; T = terrestrial mammals; B = bats; H = hornbills.

dispersed figs of forest trees (*F. variegata*, *F. fistulosa*) are very similar in this respect. The bat-dispersed (and arboreal-mammal-dispersed?) figs of *F. annulata* and *F. depressa* have relatively small crops which are rapidly depleted by frugivory (although large numbers also fall to the ground), but are produced less frequently than most bird-dispersed species.

Crop persistence: are figs unusual?

Crop persistence is an important indicator of daily fruit availability: the shorter the duration, the greater will be the mean proportion of fruits available per day during the fruiting period. Although no quantified observations were made, other bird-dispersed plant species at Kuala Lompat generally bore fruit for much longer periods of time than *Ficus*. Detailed data on the crop persistence of bird-dispersed fruits in South-east Asia are provided by Leighton (1982), who estimated crop persistence for hornbill-dispersed trees and vines to within 5 days. The crop persistence of seventy-five tree species (excluding *Ficus*) known to be important to a wide variety of birds (i.e. not just hornbills) ranged from 25 to 83 days, with a mean value of 38 days. Assuming that these values of crop persistence are typical for bird-dispersed trees in the Malaysian region, *Ficus* form a unique subset because of their short crop persistence. Seventy to eighty per cent of bird-dispersed *Ficus* species have crops which usually ripen and are eaten or fall in under 14 days.

Seasonal availability of bird-dispersed fruits

In general the phenological results of this study are consistent with those of other studies: *Ficus* exhibit both intra- and interspecific aseasonality of fruiting phenology throughout the tropics (McClure 1966; Medway 1972; Crome 1975; Newton & Lomo 1979; Raemaekers, Aldrich-Blake & Payne 1980; Wharton, Tilson & Tilson 1981; Leighton 1982; Foster 1982; Milton *et al.* 1982; Leighton & Leighton 1983; Corlett 1984, 1987; Beehler 1985; Estrada & Coates-Estrada 1985; van Schaik 1986; Windsor *et al.* 1989; Michaloud, in press). However, is fruiting aseasonality really an unusual trait for the subset of forest trees with bird-eaten fruits?

In the Asian tropics, seasonal community peaks in fruit production have been demonstrated by Medway (1972), Leighton (1982) and van Schaik (1986), and more specifically at Kuala Lompat by Raemaekers, Aldrich-Blake & Payne (1980) and Bennett (1983). In contrast, Putz (1979) detected no strong fruiting seasonality in his 4-year study of canopy trees at Bukit Lanjan, Malaysia, and Wong (1983) found that understorey shrubs and trees and subcanopy trees at Pasoh, Malaysia, exhibited aseasonal fruiting.

Whatever the overriding community rhythm, past community studies of fruiting phenology in South-east Asian forests have treated all trees as equal and not partitioned phenological samples into subsets according to their seed-dispersal syndrome. Exceptions were the studies of Leighton (1982) and Leighton & Leighton (1983), which provide evidence of seasonality of fruiting by bird-dispersed plant species in East Kalimantan. The availability of lipid-rich and sugar-rich fruits, although highly variable in time, was marked with a distinct peak and a long period of fruit scarcity.

However, Leighton's (1982) study concentrated on Bucerotidae (hornbills), and his data show that of the seventy-five plant species (excluding *Ficus*) with fruit dispersed by a diversity of bird species, about 80% were highly synchronous fruiters at the species level, but only 44% at the community level (see Table 8 in Leighton 1982). In other words, less than half of the tree species important to a wide variety of frugivorous birds actually fruited during the peak of community fruiting. Thus, bird-dispersed species of the Annonaceae (mostly climbers), Myristicaceae and Meliaceae, as well as a number of bird-dispersed species of Lauraceae, and single bird-dispersed species from the Magnoliaceae, Gnetaceae, Rosaceae, Bombacaceae and Cornaceae (Leighton 1982) all, like *Ficus*, provided fruit crops outside the major community fruiting peak. At Kuala Lompat, some bird-dispersed species from the Euphorbiaceae and Myrtaceae are also known to be aseasonal fruiters (Raemaekers, Aldrich-Blake & Payne 1980).

Nevertheless, in contrast to bird-dispersed *Ficus*, most of these species are relatively rare (Leighton & Leighton 1983) and fruit at relatively long intervals (Leighton 1982), so that in comparison with figs they represent scarce fruit resources. For instance, Medway's (1972) phenological sample of sixty-one canopy trees contained only four that were important to avian fruit consumers. Of these, two were *Ficus* (*F. sumatrana* and *F. virens*), whilst the other two were *Santiria laevigata* (Burseraceae). Mean fruiting intervals for these three species over a 9-year period were approximately 5, 14 and 27 months, respectively.

In addition, many bird-dispersed tree species provide small crops relative to *Ficus* (Raemaekers, Aldrich-Blake & Payne 1980), and even when they have large crops the proportion of ripe fruit at any one time will be low (this is a logical consequence of long crop persistence time).

Finally, frugivorous birds such as members of the Dicaeidae (flowerpeckers), *Irena puella* (fairy bluebirds) and some of the Pycnonotidae (bulbuls) may not be able to eat many of the fruits available because of their small gape size. Such birds can only eat from fruits larger than their gape if they are succulent enough to be broken piecemeal while still attached to the tree. Bird-dispersed figs are unusual in that most can be harvested by smaller birds, irrespective of fig size.

Thus, although frugivorous birds may be able to find non-fig fruit crops throughout the year, crops available during periods of general scarcity may nevertheless be rare, small and possess relatively few ripe fruit. Such crops are likely to be heavily exploited and therefore rapidly depleted. In such a situation *Ficus* will be of critical importance to fruit-eating birds, because their phenological patterns, large crop sizes, relative numerical abundance and ease of harvesting guarantee year-round fig availability, even in small patches of lowland forest. When in fruit, the strong intra-crown synchrony of fig ripening provides a bountiful supply of sugar-rich fruit. Birds can therefore spend long periods of the day at individual fig sources (see Lambert 1989c). It is a combination of these attributes, rather than intra-population fruiting asynchrony *per se*, which makes *Ficus* a unique and extremely important subset of the bird-dispersed fruit resources in South-east Asian lowland forests.

Large-fruited bird-dispersed *Ficus* are an exception because of their rarity. This may have important consequences for birds such as *Treron capellei* (large green pigeon), which specializes on large figs as a food source (Lambert 1989b): large-fruited *Ficus* tend to grow on large trees of commercially important species, and are likely to be severely depleted by selective logging activities (Lambert 1987).

Fig availability and fruit scarcity

For *Ficus* to act as a keystone resource for frugivorous birds, fig crops must be available at times when other fruit resources are rare. Unfortunately, non-fig resources of importance to birds were not monitored during this study, and it is therefore impossible to determine whether figs were most abundant at times of general fruit scarcity.

Phenological data collected at Kuala Lompat in 1975 (Raemaekers, Aldrich-Blake & Payne 1980), however, show that fruit was most scarce that year during July, September and October. In these months there were at least eight, fourteen and twelve ripe fig crops, respectively, in 67 ha of forest. During the same year, figs were most scarce during November, at a time when other fruit resources were more abundant. The fig crops monitored by Raemaekers, Aldrich-Blake & Payne (1980) were those visited by primates, and, although not identified to species, were probably bird-dispersed species because the majority of species with figs eaten by primates at Kuala Lompat are also eaten by birds (Lambert 1990).

Raemaekers, Aldrich-Blake & Payne (1980) and Bennett (1983) also show that at Kuala Lompat a major annual community peak of tree fruiting usually occurs within the period May–August. Whilst the general rule for intraspecific fruiting by bird-dispersed *Ficus* at Kuala Lompat is one of asynchrony, there is evidence that the fruiting of some species during the 3 years of this study was more synchronous. The period when the latter species tend to fruit, February–April, is before the usual major peak of community fruiting. Maximum availability of these figs therefore occurs at a time of relative fruit scarcity. This period is also, although perhaps coincidently, during the same calendar months as those in which Raemaekers, Aldrich-Blake & Payne (1980) recorded a prolonged period of fruit scarcity, between December and April 1976.

Data therefore suggest that figs can be considered as keystone resources from the point of view of their seasonal availability. It is clear that figs are most abundant at a time when other fruits are relatively scarce. There may, however, be periods when figs are locally scarce, such as during November 1986 at Kuala Lompat. During such times, frugivores with small home ranges may have to depend on other keystone resources, such as those identified by Leighton & Leighton (1983). However, minor fig crops could also play an important role as a fruit resource during periods of fruit scarcity, in particular for smaller-bodied frugivores such as Dicaeidae (flowerpeckers), which weigh between 7–10 g.

There is one additional piece of evidence which demonstrates that *Ficus* can support frugivores all year round, implying keystone status. This is that *Ficus* is the only known plant taxon upon which frugivorous birds in South-east Asia have specialized. *Treron* spp. (forest green pigeons) and probably some *Megalaima* spp. (barbets) are fig-eating specialists (Leighton & Leighton 1983, Lambert 1989a, 1989b), whilst *Rhinoplax vigil* (helmeted hornbills) depend almost exclusively on *Ficus* for the fruit component of their diet (Leighton 1982, A. Johns pers. comm.).

Ficus *density and avian ranging behaviour*

Ficus spp. appear to have the potential to sustain frugivores during periods of fruit scarcity in some tropical forests but in Makokou forest, Gabon, Gautier-Hion and Michaloud (1989) found that this was not the case. Whilst twenty-six of thirty-eight *Ficus* species at Kuala Lompat are stranglers (Lambert 1989a), only five of twenty species in Gabon have this growth-form. Furthermore, not only are *Ficus* which produce large crops (i.e. stranglers) relatively rare in Gabon, but they fruit at relatively long intervals of 1–3 years. The rarity of stranglers in Makokou is perhaps the major reason why *Ficus* there are unimportant fruit resources for birds. The majority of *Ficus* species at Makokou appear to have fruiting characteristics similar to those of Malaysian *F. annulata* and *F. depressa* and, like these species, only appear to be important fruit resources for bats.

Gautier-Hion & Michaloud (1989) also suggest that *Ficus* spp. at Makokou are important only to frugivores with large home ranges. On a 1-day census they found five *Ficus* plants with ripe fruits in 100 ha. At Kuala Lompat, there were between two and thirty bird-dispersed *Ficus* with ripe figs month^{-1} in 74 ha, which translates to perhaps anything between one and thirteen *Ficus* per 100 ha with ripe figs on any particular day.

Although the density of fig resources may therefore at times be lower at Kuala Lompat than at Makokou, typical crop sizes are larger at the former site. Nevertheless, for frugivores to be dependent on figs in South-east Asia, or to rely on them at certain times, they need to be wide-ranging. The limited data available on ranging behaviour suggests that this is indeed true. A radio-tagged *Megalaima henricii* (yellow-crowned barbet), a species thought to be a fig specialist (Lambert 1989a), regularly flew over 700 m from its roost site to a fruiting *Ficus binnendykii* at Kuala Lompat, and spent between 71% and 85% of its time foraging at that tree (Lambert 1989c). If it is assumed that the bird could potentially range over similar distances in any direction, its total home range is likely to exceed 150 ha. The same study showed that different *Calyptomena* species (green broadbills) ranged over areas of about 13 ha week^{-1} in March 1986 when figs were relatively abundant, and 24 ha week^{-1} during April 1986 when figs were rarer. These birds spent between 31% and 50% of their time at fruiting *Ficus*.

Ficus spp. may not be keystone species for frugivorous birds with small home ranges, because figs can occasionally be locally scarce at times of general scarcity. Most obligate frugivores in the Sundaic region, however, are larger species which range over very large areas. Hornbill species that include large quantities of figs in their diets are known to range over areas of between 280 ha and 1500 ha (Leighton 1982, P. Poonswad, pers. comm.). *Treron* spp., which are entirely dependent on figs (Leighton 1982, Lambert 1989a, 1989b), are nomadic and apparently range over huge areas (P. R. Wells, personal communication).

Hornbills are the only South-east Asian frugivorous birds for which a relatively detailed knowledge of home-range size exists. Knowing that they feed almost exclusively on figs larger than 12 mm in diameter (Lambert 1989a), it is possible to estimate the number of fruit crops that might be encountered in an area encompassing their minimum home range. A hornbill ranging over 280 ha of lowland forest would potentially be able to visit about 280 fig crops with suitably sized figs per year. In an average month there would be about twenty-three fig crops with ripe fruit in its home-range area, whilst in some months more than fifty crops could be visited. In poor months, however, very few crops might be available. In November 1986, for instance, there were no medium- or large-fruited figs in the 74-ha phenological sample area at Kuala Lompat. Although it is probably unrealistic to assume that there would have been no crops in this fig-size category in an area of 280 ha, these data do suggest that at such times hornbills may have to rely on smaller figs. Small figs, which are very occasionally eaten by large hornbills (Lambert 1989a), would have provided around eight crops in 280 ha during November 1986.

Thus, although *Ficus* bearing ripe fruit may be widely scattered at certain times, specialized frugivorous bird species in South-east Asia appear to range over large enough areas to enable them to find fruiting *Ficus* at any time.

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