

OBSERVATIONS OF FRUGIVOROUS BIRDS AT FRUIT-BEARING PLANTS IN THE NORTH NEGROS FOREST RESERVE, PHILIPPINES

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Abstract. Fruit-bearing plants do not only serve as seed sources for forest regeneration but also as important foci for the re-establishment of other plant species by attracting seed-dispersing birds to their vicinity. The behavior of 19 species of avian visitors at 16 fruit-bearing plant species in a montane old growth forest on the Philippine island of Negros was observed to determine their potential quality as seed dispersers. Behavioral observation included frequency and duration of visits by each forager and its fruit-handling techniques. All bird species handled fruit in a way compatible with effective seed dispersal. Obligately frugivorous bird species spent significantly more time in a food tree than partial frugivores, thus increasing the chance that ingested seeds were deposited by defecation or regurgitation beneath the parent tree. Conversely, the partial frugivores in this study often joined fast and far-traveling monospecific and/or mixed-species flocks, thus carrying seeds away from the parent plant. Therefore, the partial frugivores should be better potential seed dispersers than the obligately frugivorous bird species. The highest visitation rates and numbers of fruit-eating birds were recorded at fig trees, confirming their important resource role for tropical frugivores. Small fruits were consumed by a variety of fruit-eating birds, especially passerines with mixed diets, whereas large-fruited and large-seeded fruits were only dispersed by a few large and obligately frugivorous birds. We do not interpret this relationship as a result of coevolution, since our findings suggest the obligate frugivores to be poorer seed dispersers. The consumption of large fruits by only a few avian frugivores is probably limited by gape width, but even below this size limit the evolution of specialized seed dispersal systems should not necessarily be determined solely by size of fruits and their consumers. *Accepted 17 September 1999.*

Key words: *Frugivory, Philippines, seed dispersal, fruit-eating birds, dispersal quality, fruit size, conservation.*

INTRODUCTION

Much of the rainforest in the Western Visayas of the Philippines, especially on Negros, has been cleared for agricultural use, the timber industry and charcoal production. In the North Negros Forest Reserve (NNFR) less than 20% of the area is actually forested (Diestel in Curio 1996), and fragments of primary forest remain on steep, hardly accessible slopes. Most of the rainforest plants in the NNFR bear fleshy fruits and are thus potentially dispersed by birds and fruit bats (Hamann & Curio 1999). Fleshy-fruited plants may serve not only as seed sources for forest regeneration but also as important foci for the re-establishment of other plant species by attracting seed-dispersing birds to their vicinity (McDonnell & Stiles 1983).

One of the central problems in seed dispersal research is the distinction of 'good' and 'poor' seed

dispersers. Quantitative tests devoted to the recruitment success of animal-dispersed plants have shown that seeds or seedlings near fruiting adults fare less well than members of a cohort a few to a few tens of meters away (Howe 1993). This 'escape advantage' may be due to higher progeny mortality because of herbivores normally feeding on adults (distance-effect), or disproportionate seed or seedling predation by density-responsive seed-eaters and pathogen infestation (but see Schupp 1988), or to competition for nutrients within the same cohort under the parent tree (reviews by Clark & Clark 1984, Howe 1986, Augspurger 1988). In quantitative terms, an ideal avian disperser visits the food plant frequently and reliably, and leaves the plant before defecating or regurgitating the ingested seed (Schupp 1993). Qualitatively, an effective disperser does not destroy seeds during fruit handling and ingestion, and will carry the seeds to appropriate sites for germination and growth (Green 1993, Schupp 1993). Schupp (1993) provides evidence that in some systems qua-

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lity is the dominant component of a disperser's effectiveness. Furthermore, the dispersal efficiency of a bird which is not able to mash fruits, but has to swallow them whole, will depend on the size of the bird's gape relative to the size of fruits and seeds. Large-fruited or large-seeded plants might thus be expected to have a narrower range of potential dispersers (Hamann & Curio 1999). Only if we know more about the potential dispersal efficiency of different dispersers is an understanding of selection on fruit traits and of coevolution possible. However, the problem of good and poor dispersers, with respect to dispersal sites, will only hold for plants which require specific sites for successful recruitment. If these sites emerge unpredictably then any disperser removing seeds and distributing them at optimal densities will be a good disperser. Howe & Estabrook (1977) and Howe & Smallwood (1982) suggested a paradigm (but see Howe 1993 for a critical review) of suites of character combinations regarding specialization and generalization among avian frugivores and tropical trees. According to the paradigm, large-seeded trees have nutritious and energy-rich fruits, which they produce in small numbers during an extended fruiting season, and seed dispersal to appropriate germination sites is critical for their recruitment (Howe & Estabrook 1977, Howe & Smallwood 1982). They rely mostly on a few large, obligately frugivorous birds that utilize a few fruit species per day. In contrast, small-seeded trees produce many small, less energy-rich fruits during a sharply peaked fruiting season. According to the paradigm, in this case seed dispersal to specific sites may not be critical for recruitment, since many seeds are dormant and can wait for the opportunity to germinate in a newly opened gap, or are resistant to density- and/or distance-dependent mortality. Thus, they attract many facultatively frugivorous bird species of small body size to a superabundant food source; the birds may switch opportunistically among many fruiting tree species and complement their insect diet with fruits.

The major aim of this study was to obtain data on guild composition and food preferences of avian frugivores in the NNFR as a baseline from which to launch an in-depth study on seed dispersal of fruit-bearing rainforest plants. To this end, frequency and duration of avian visits to fruiting plants were recorded and fruit-handling techniques (swallowing or dropping fruit or pecking parts out of it) described. Based on these data, fruit-eating birds were ranked

according to their seed-dispersal abilities. More specifically, we asked the question whether the large-seeded among the large-fruited species were visited by fewer disperser species than were plants with fruits or seeds that are more easily swallowed; according to Hamann & Curio (1999) seed size and fruit size of trees in the NNFR are positively correlated.

STUDY AREA AND METHODS

The main part of the study was conducted within an upland tropical rainforest near Patag, Silay City district, on the island of Negros (10°41'N, 123°11'E), Philippines. This area is located on the northwestern slope of Mt. Mandalagan (Fig. 1) at an average elevation of 1000 m a.s.l. within a 24 km² patch of montane old growth forest northwest of Mt. Mandalagan (Hamann & Curio 1999). The study took place during the rainy season, which in this region lasts from May to mid-January. Additional data from one further tree species (*Elaeocarpus* sp.) were obtained during a 5-day visit to a montane study site near Guintubdan, La Carlota district (10°25'N, 123°05'E, 820 m a.s.l.; Fig. 1), on the western slope of Mt. Kanlaon volcano. Both habitat characteristics and climate resemble those of the study area near Patag.

Growth form and fruit characteristics of the plant species selected for study, as well as time of year and duration of observations for each species, are presented in Table 1. Many plant species have so far only been identified to their generic level (see Hamann *et al.* 1999, in press). To avoid confusion, this paper uses Ilongo-names in quotation marks for the fig species. In this study the seeds of *Aglaia* sp. are considered equivalent with fruits since they are covered by a thin nutritious skin which is presumably used by frugivores. Plant species were divided into three groups of differing fruit size: large-fruited (fruit larger than 15 mm maximum width, containing a single large seed), small-fruited (fruit smaller than 15 mm, with one or a few seeds), and fruits of any size with very soft flesh containing many tiny seeds (Moraceae, *Melastoma affine*). A frugivore presumably swallows seeds even when it ingests only parts of a Moraceae or *Melastoma affine* fruit, and these plant species were sufficiently soft-skinned for bills to penetrate. The size of their fruits should therefore have little effect on the array of potential disperser species.

Observations were made from mid-August until end of November 1996. Days with strong wind

(typhoon) and rain were skipped. Observation time was evenly distributed over daylight hours (between 06:00 and 18:00 h). But due to inclement weather conditions (rainy season) it was impossible to follow a consistent daytime schedule of observations. Therefore, each hour of observation enters into the analysis on the assumption that bird activities and avian visitation rates were independent of time of day. However bird activities varied among trees with respect to time of day, so that whole-day observations would have been necessary to obtain data representing the whole range of visitation rates at each individual plant. This was impeded by the lack of manpower.

Records of each avian visit to a tree included bird species, duration of visits scored in 5-min timeclasses

(see below), and fruit handling method (swallowing fruit whole, pecking parts out of it, dropping fruit). Since it was impossible to identify birds individually (especially in flocks), repeated visits by the same individual had to be treated in the same way as visits by different birds. Very often the precise moment when birds arrived at and/or flew out of a tree could not be determined. Therefore it was assumed that a bird's presence and absence was noticed soon after its entry and/or departure, so that the duration of all visits was scored to the nearest 5 min.

To demonstrate differences in visits lengths among bird species, we pooled results across all visited plant species within the defined fruit size classes (see above). Due to sample size only visit lengths to fig trees (Moraceae) were tested statistically with the

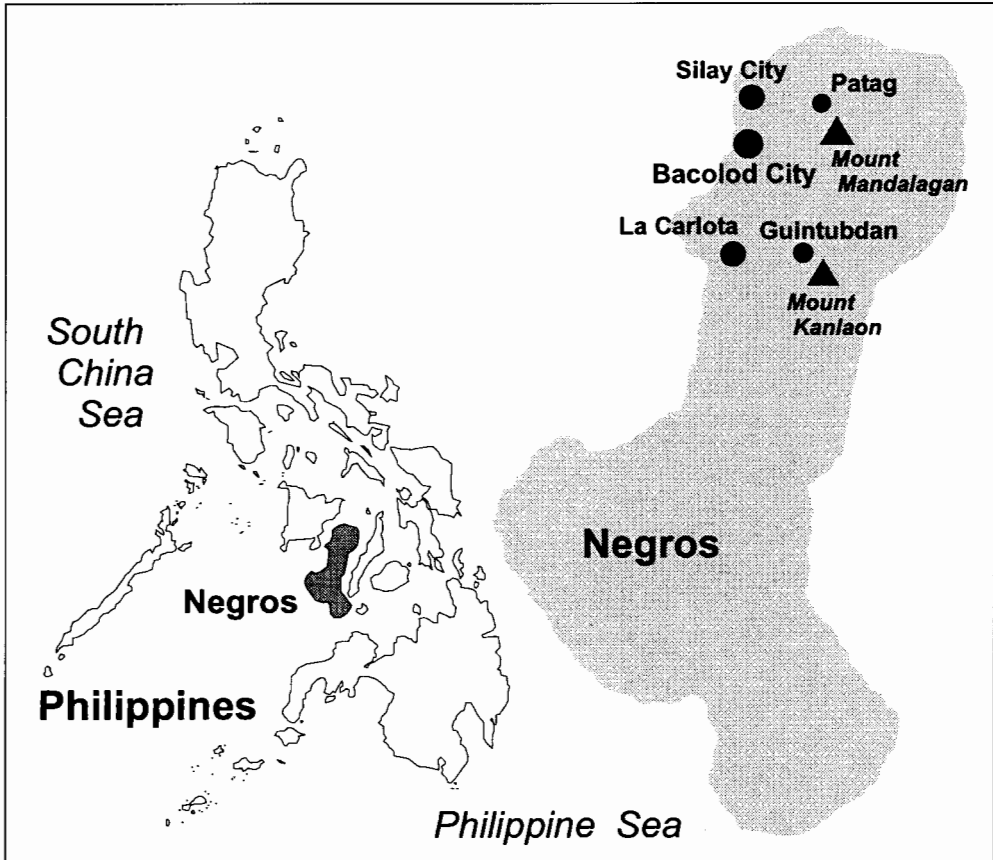


FIG. 1. Location of study sites on Negros: Patag, on the northwestern slope of Mt. Mandalagan; Guintubdan, on the western slope of Mt. Kanlaon.

TABLE 1. Growth form, fruit and seed characteristics of the fruit-bearing plants selected for study.

Nr.	Fruit-bearing plant (Illego name in '...')	Growth form	Fruit mean max. width \pm SD (mm)	Seed mean max. width \pm SD (mm)	Number of seeds in fruit	Fruit color / Fruit position	Estimated crop size (extensive > rich > medium)	Elevation / Total hours / Months when observed
1	Moraceae <i>Ficus irisana</i>	small tree (dbh < 10 cm midstory)	6.6 \pm 0.46 n = 10	< 1	many tiny	orange / on petiole	medium	815 m / 12 h / November
2	Moraceae <i>Ficus</i> sp. (‘Dalakit a’)	strangler fig (canopy)	11.2 \pm 0.68 n = 25	< 1	many tiny	dark red / on short petiole	extensive	820 m / 42 h / September
3	Moraceae <i>Ficus</i> sp. (‘Dalakit b’)	strangler fig (canopy)	10.5 \pm 0.65 n = 18	< 1	many tiny	dark red / on short petiole	extensive	845 m / 52 h / September
4	Moraceae <i>Ficus</i> sp. (‘Dalakit c’)	strangler fig (canopy)	10.5 \pm 1.12 n = 23	< 1	many tiny	dark red / on short petiole	extensive	840 m / 16 h / September
5	Moraceae <i>Ficus</i> sp. (‘Lunok a’)	strangler fig (canopy)	19.4 \pm 2.66 n = 17	< 1	many tiny	orange to red / on petiole	extensive	860 m and 840 m / 24 h and 55 h / August and October, November
6	Moraceae <i>Ficus</i> sp. (‘Lunok b’)	strangler fig (canopy)	12.1 \pm 2.74 n = 34	< 1	many tiny	whitish yellow / on short petiole	extensive	915 m / 21 h / October
7	Melastomataceae <i>Melastoma affine</i>	small tree (dbh < 10 cm understory)	11.2 \pm 1.06 n = 26 (subfruit)	< 1	many tiny on surface	red / on petiole, composed of 5 subfruits	medium	800 m / 3 h / August, September
8	Araliaceae <i>Schefflera octophyllum</i>	climber (canopy)	3–4 (estimate)	< 1	some tiny	red / on short petiole, in racemes	rich	790 m / 14 h / November
9	Pandanaceae <i>Pandanus</i> sp.	climber (subcanopy)	4–5 (estimate)	< 1	some tiny	red / on petiole, cob-shaped, multiple-fruit	medium	800 m and 845 m 2 h and 52 h / August, September

10	Myrtaceae <i>Syzygium</i> sp.	tree (subcanopy)	6.6 ± 0.88 n = 17	6.3 ± 1.06 n = 2	single	dark red / on petiole	medium	850 m / 8 h / August 950 m / 3 h / August 860 m / 39 h / October, November
11.	Elaeocarpaceae <i>Elaeocarpus</i> sp.	tree (canopy)	7.9 ± 0.65 n = 9	5.5 ± 0 n = 2	single	dark blue / on petiole	rich	
12	Burseraceae <i>Canarium asperum</i>	tree (canopy)	12.3 ± 0.85 n = 25	11.5 ± 0.94 n = 4	single	blue-violet / on petiole	rich	
13	Burseraceae <i>Canarium villosum</i>	tree (canopy)	19.3 ± 1.5 n = 26	15.5 ± 1.17 n = 10	single	blue-violet / on petiole	medium	840 m / 6 h / October, November
14	Meliaceae <i>Aglaita</i> sp.	tree (canopy)		33.2 ± 1.76 n = 18	four-chambered pericarp, encompassing 4 seeds	beige-brown shell, scarlet-red seeds / on petiole	rich	800 m / 40 h / August, September
15	Icacinaceae <i>Platea excelsa</i>	tree (canopy)	36.3 ± 2.69 n = 22	34.8 ± 1.17 n = 9	single	red / on petiole	extensive	840 m / 25 h / November

Mann-Whitney U-test. To compensate for the multitude of pairwise comparisons, significance level was adjusted by Bonferroni correction ($P_{adj.}$). It is to be expected that avian behavior depends on the characteristic physiognomy and growth form of each visited fruiting plant, its fruit crop size, and the mass and nutritional value of its fruits. However the main focus of this analysis was to obtain general patterns of frugivore behavior in fruiting plants; the potential influence of the individual plant species on foraging behavior was therefore neglected (see also Green 1993, Pratt & Stiles 1983).

Mean number of frugivore visits per hour for each plant species are the sum of the total number of visits per observation hour divided by the total hours of observation. The database for the analysis of differences in visitation rates among plant species were the total numbers of visits by dispersers per observation hour. Data were log-transformed to reduce heavy skew, and analyzed by one-way analysis of variance (Sokal & Rohlf 1981). Afterwards, pairwise comparisons between plant species were performed with a multiple range test (Fisher's least significant difference procedure). Differences in visitation rates within selected fig trees between predefined groups of bird taxa (see Results) were tested by a Paired Student's t-test (Sokal & Rohlf 1981).

It should be noted that only one individual of each plant species (except 'Lunok a' and *Pandanus* sp., see Table 1) enters into the analysis. Sampling bias might therefore have affected the fig species 'Lunok b', at which unexpectedly low visitation rates and low numbers of disperser species were observed. The investigation of more fruiting individuals per plant species was impeded by the fact that only one fruiting individual of a plant species could be found, or that others were not accessible due to the rough topography of the study site, or that the periphery of the crown of the focal tree was hidden from view by the canopy of neighboring trees.

RESULTS

The frugivores. A total of 19 species of birds were observed foraging in 16 different species of fruit-bearing plants. An additional bird species, *Dicaeum ignipectus*, was observed feeding on the berries of an unidentified mistletoe species of the family Loranthaceae. Table 2 gives an overview of the avian frugivores and the plant species on which they fed. All bird species were resident on Negros. Typical frugivores

TABLE 2. Avian frugivores and fruit-bearing plant species in which they were observed foraging.

Bird species	body mass ¹	diet ² / grouping ³	Fruit bearing plants (llonggo-name in '...')														
			<i>Ficus iricana</i>	<i>Ficus</i> sp. ('Dalakit a')	<i>Ficus</i> sp. ('Dalakit b')	<i>Ficus</i> sp. ('Dalakit c')	<i>Ficus</i> sp. ('Lunok b')	<i>Ficus</i> sp. ('Lunok a')	<i>Melastoma affine</i>	<i>Schefflera octuplyllum</i>	<i>Pandanus</i> sp.	<i>Syzygium</i> sp.	<i>Elaeocarpus</i> sp.	<i>Canarium asperum</i>	<i>Canarium villosum</i>	<i>Platea excelsa</i>	<i>Aglaita</i> sp.
Columbidae (pigeons and doves)																	
<i>Phapitreron leucotis</i>	108 g	of,g/s,sg	+	+							+	+					
<i>Ptilinopus occipitalis</i>	238 g	of/s,sg		+	+	+		+			+			+	+		
<i>Ptilinopus leclancheri</i>	162 g	of/s,sg												+			
<i>Ducula poliocephala</i>	537 g	of/s,sg		+		+	+	+							+	+	+
<i>Macropygia phasianella</i>	180 g	of/s,sg									+						
Psittacidae (parrots)																	
<i>Loriculus philippensis</i>	35 g	of,g/s,sg		+		+		+			+						
Capitonidae (barbets)																	
<i>Megalaima haemacephala</i>	ca. 40 g	of/s,sg		+	+	+		+									
Bucerotidae (hornbills)																	
<i>Penelopides panini</i>	512 g	f,i./s,sg															+
Campephagidae (cuckoo-shrikes)																	
<i>Coracina striata</i>	111 g	i,f/sg					+										
Oriolidae (orioles)																	
<i>Oriolus steerii</i>	56 g	i,f/s					+										
Rhabdornithidae (creepers)																	
<i>Rhabdornis mystacalis</i>	25 g	i,f/mf		+	+	+					+						
<i>Rhabdornis inornatus</i>	39 g	i,f/mf				+	+						+				
Pycnonotidae (bulbuls)																	
<i>Hypsipetes philippinus</i>	39 g	i,f/mg		+	+	+	+		+		+	+	+	+	+	+	+
Muscicapidae (flycatchers)																	
<i>Eumyias panayensis</i>	20 g	i,f/s,mf		+	+	+								+			
Sturnidae (starlings)																	
<i>Sarcops calvus</i>	142 g	i,f/s,sg				+	+		+		+			+			
Dicacidae (flowerpeckers)																	
<i>Dicaeum bicolor</i>	8 g	f,i./sg,mf		+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Dicaeum trigonostigma</i>	7 g	f,i./sg,mf				+					+	+	+				
Zosteropidae (white-eyes)																	
<i>Zosterops montanus</i>	11 g	i,f/lg,mf		+	+	+	+	+	+		+		+				+
<i>Zosterops nigrorum</i>	no info.	i,f/lg,mf									+	+					

¹ Data on body mass (rounded to the nearest gram) are taken from the CRC Handbook of Avian Body Masses (ed. by Dunning, 1993)² Diet: of: obligately frugivorous, g: granivorous, f: frugivorous, i: invertebrates³ Grouping: s: solitary, sg: small conspecific groups, lg: large conspecific groups, mf: mixed-species flocks

were the Columbidae, Psittacidae, Bucerotidae, Capitonidae, Pycnonotidae, and Dicaeidae, with the latter four families complementing their diet regularly with small animals (mainly arthropods). Several bird species not normally regarded as frugivores were seen to eat fruits: both *Rhabdornis* species, *Zosterops montanus* and *Z. nigrorum* (Zosteropidae), and *Eumyias panayensis* (Muscicapidae). Especially Zosteropidae and Muscicapidae are considered to be typical insectivores.

Bird behavior at fruiting trees. The Columbidae entered a fruiting tree singly or in groups of up to ten individuals (*Ptilinopus occipitalis* in 'Lunok a', *Ducula poliocephala* both in 'Lunok a' and *Aglaia* sp.). *Hypsipetes philippinus* (up to 15), *Zosterops montanus* (up to >10, in 'Dalakit b' up to >50), and *Dicaeum bicolor* (up to >10) were commonly seen in flocks of varying sizes. The other species arrived mainly as singles (*Eumyias panayensis*), pairwise, or in small groups (up to 5, but flocks of about 30 *Rhabdornis inornatus* were observed in 'Dalakit c'). The Rhabdornitidae, *Zosterops montanus*, *Eumyias panayensis*, and the Dicaeidae were often seen together in mixed-species flocks moving through the canopy and staying in a particular fruiting tree for a relatively short time (see also Fig. 2).

Techniques of handling fruit varied among bird species. Fruits were plucked while the bird was perched and swallowed whole (by Columbidae, *Coracina striata*, Rhabdornitidae, *Sarcops calvus*) or mashed between the mandibles and then swallowed (*Megalaima haemacephala*). *Hypsipetes philippinus* regularly took fruits on the wing, held them in its bill and swallowed them whole after landing on a branch. *Eumyias panayensis* did so exclusively, and *Rhabdornis mystacalis* at times. Snatching fruits in flight enabled the birds to reach fruits on the periphery of the canopy, where twigs did not permit perching. Dicaeidae and Zosteropidae only pecked pieces of flesh out of those fruits which were too large to be swallowed whole, a technique also employed by *Sarcops*. Smaller fruits were mandibulated and mashed before swallowing. *Loriculus philippensis* treated the fruits in the same manner although its bill appeared large enough for most of the fruits (except for those of 'Lunok a'). On rare occasions it could be observed that fruit was picked and carried well out of sight (*Hypsipetes philippinus*, Dicaeidae, Rhabdornithidae).

It was impossible to record the distance a bird traveled after leaving a fruiting tree. But there was

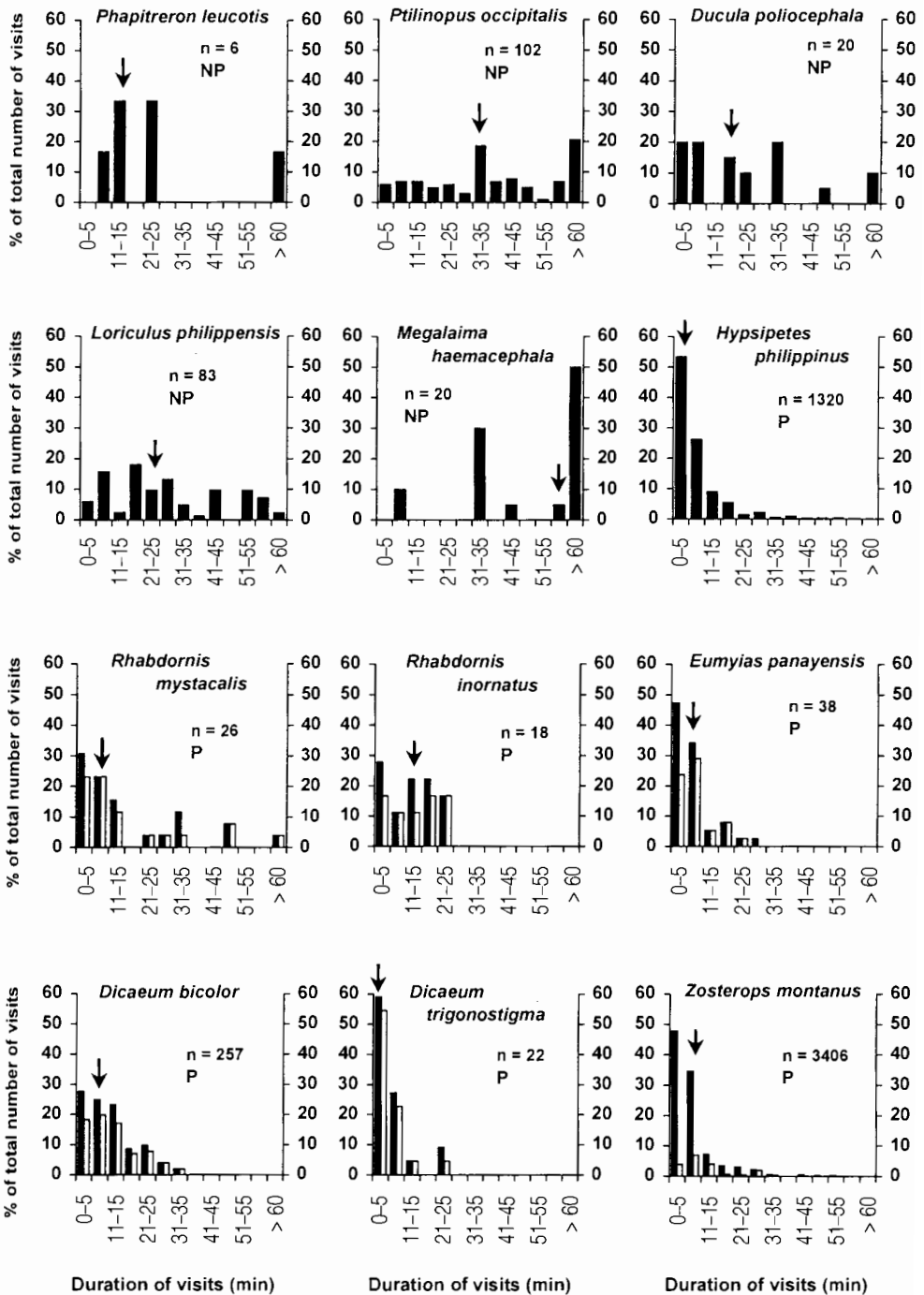
evidence (bird calls, sight records) that individuals of *Hypsipetes philippinus*, *Ptilinopus occipitalis*, and *Ducula poliocephala* after visiting often stayed in the vicinity of the tree, making repeated visits.

We have no first-hand information on how seeds are processed by a bird, e.g., defecated whole or digested and destroyed, and whether seeds are dispersed to appropriate places (but see Discussion). Therefore by taking only the observed fruit handling into account, all avian frugivores in Table 2 can be considered as potential dispersers for the plant species in which they were seen foraging. As a rule, fruits were consumed whole, even after prior handling. Bird species ingesting only parts of a fig, leaving the rest on the tree or dropping it, might still act as dispersers since even small pieces of pulp would contain some of the many tiny seeds inside. It was never observed that seeds were regurgitated shortly after ingestion of fruit, nor that seeds were separated from the pulp and dropped under the tree. An exception is the interaction between *Zosterops montanus* and *Platea excelsa*. Seeds of *Platea excelsa* fruits are much too large to be swallowed by a Mountain White-eye. The bird only ate morsels of the pulp, thus opening the fruit to insect or microbe attack and thus desiccation, while leaving the seed on the tree. Therefore *Zosterops montanus* acts as a classical fruit thief (for definition see Green 1993) of *Platea excelsa*.

Duration of visits. Duration of visits by avian frugivores at fruiting plants was analyzed by pooling the data across all plant species within the size classes defined (see Fig. 2). Only those bird species were considered for which more than four visits to fruiting plants were observed. Plant species with low numbers of observation hours and unfavorable observation conditions were omitted from analysis.

Around 75% of visits made by passerine species to fruiting plants lasted less than 20 min (Fig. 2). Non-passerines often stayed much longer than passerines, which could be demonstrated statistically for Moraceae species. Here, each non-passerine species spent significantly more time per visit in a fig tree than any passerine (Mann-Whitney U-test, for all pairwise comparisons $P_{adj.} < 0.001$; exception: no significant difference between *Ducula poliocephala* and *Rhabdornis mystacalis*, and between *Phapitreron leucotis* and both *Rhabdornis* species). On occasion, extended visits could be observed: two visits of *Ducula poliocephala* in fig trees, and one such visit in the large-seeded *Aglaia* sp., lasted for about 1.5 h. Nine

Duration of visits to Moraceae species



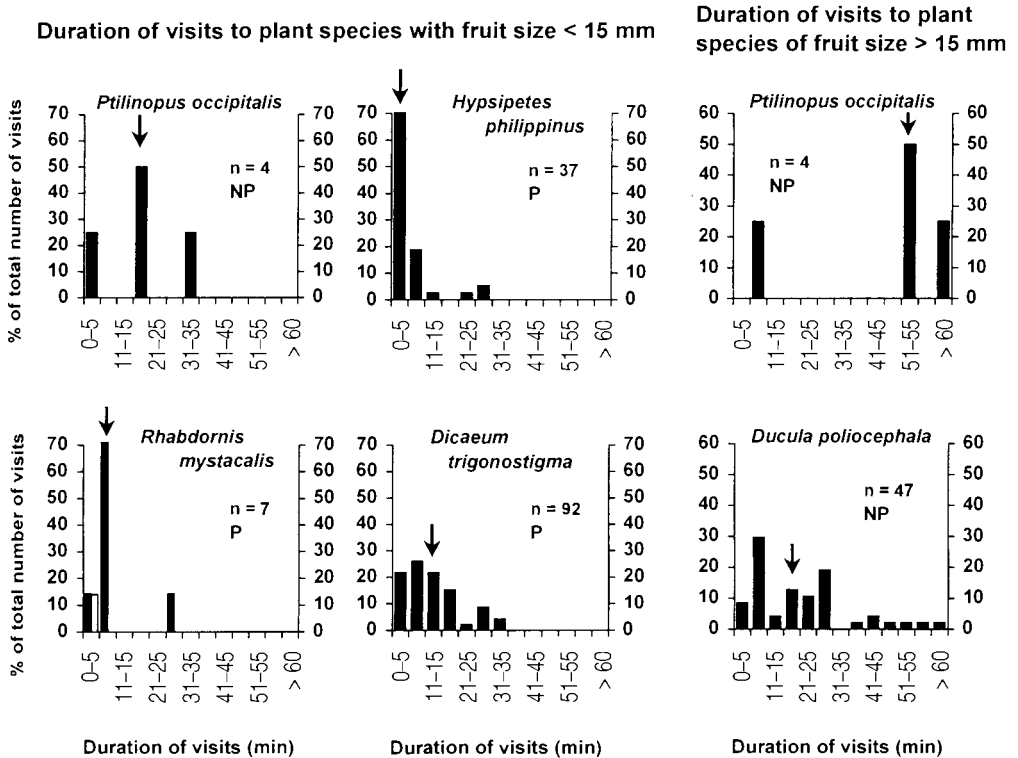


FIG. 2. Duration of visits to fruiting plants by various avian frugivores. Black bars present the percentage of total number of visits by each frugivore species that lasted as long as the corresponding 5 min time-class. White bars indicate the proportion of visits within a 5 min time-class in which a bird was a member of a mixed-species flock. Only those bird species with $n > 4$ are considered. Arrows indicate timeclass in which the cumulative percentage of all shorter visits sums up to 50%. NP denotes non-passerines, P passerines. Plant species with low numbers of observation hours and unfavorable observation conditions (e. g., canopy hidden by neighboring trees) were omitted from the analysis. According to fruit characteristics plant species are divided into three groups: Moraceae (*Ficus irisana*, 'Dalakit a', 'Dalakit b', 'Lunok a', 'Lunok b'), plant species with fruits smaller than 15 mm maximum width (*Schefflera octophyllum*, *Syzygium* sp., *Canarium asperum*), and with fruits larger than 15 mm maximum width (*Canarium villosum*, *Aglaia* sp.). Within a size class data are pooled over all plant species.

visits of *Ptilinopus occipitalis* in fig trees lasted around 2 h, and two visits more than 3.5 h. In the large-seeded *Canarium asperum*, one visit lasted around 1.5 h and two visits were of almost 1 h duration. Fifty percent of the visits (all in fig trees) of *Megalaima haemacephala* were longer than 1 h, of which four visits lasted for around 2 h and two visits more than 4 h. Except for *Loriculus philippensis*, all long visits of the non-passerines were mainly due to the long resting times between foraging bouts in the trees visited. In the Columbidae, periods of intense foraging alter-

nated with long periods of rest. In contrast, *Megalaima haemacephala* displayed a relatively cryptic behavior throughout. Moving slowly, it looked for fruits, often interrupting its search by periods of rest in which it sometimes scanned the surroundings. Conversely, all passerine species were mainly actively searching for food throughout the duration of their visits.

Visitation rates by avian dispersers. The number of disperser species that serve a given plant species declines with fruit and seed size (Fig. 3). The correlation

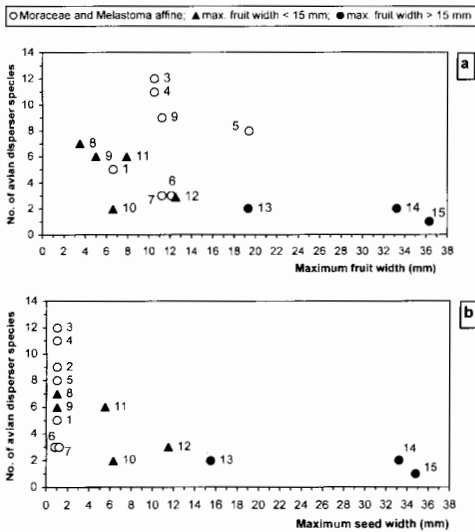


FIG. 3. Total numbers of avian disperser species plotted against (a) fruit size and (b) seed size of their food plants. Plant species are divided into three groups according to fruit size (see Methods) and numbered according to Table 1. In (a), for *Aglaia* sp. (14) maximum diameter of seed is plotted.

is significant for seed size (Fig. 3b; Spearman Rank Correlation: $r = -0.61$, $P = 0.02$). The pattern seems not to be due to an unequal number of observation hours devoted to each plant species since there is no correlation of total visitation time with total number of disperser species ($r = 0.38$, $P > 0.5$). However, to account for any possible bias of unequal observation hours, we calculated the mean number of visiting disperser species per hour for each plant species in Fig. 4 (see reasoning there) and correlated them with fruit and seed size. Again, the correlation is significant only for seed size (Spearman Rank Correlation: $r = -0.64$, $P = 0.03$).

Fig. 4 depicts the mean number of visits by dispersers per hour. Visitation rates (using total number of visits across all disperser species) differed significantly among plant species (ANOVA: $F_{10,303} = 81.2$, $P < 0.001$). Pairwise comparisons revealed significant differences among plants (Fisher's least significant difference procedure, $P < 0.5$). The fig species 'Dalakit a' and 'Dalakit b' attracted the highest numbers of visits by avian frugivores per hour. Even the larger-fruited fig 'Lunok a' still attracted signifi-

cantly more visits of dispersers per unit time than did any non-Moraceae species except for *Schefflera octophyllum* (see below). 'Dalakit a' and 'Dalakit b' were mainly exploited by flocking passerines (see Fig. 4; 'Dalakit a', paired t-test: $t_{41} = -6.5$, $P < 0.001$; 'Dalakit b', t-test: $t_{51} = -17.4$, $P < 0.001$) and by *Hypsipetes philippinus* ('Dalakit a', paired t-test: $t_{41} = -11.0$, $P < 0.001$; 'Dalakit b', paired t-test: $t_{51} = -21.1$, $P < 0.001$). In contrast, 'Lunok a' was visited significantly more often by non-passerines than by flocking passerines (paired t-test: $t_{54} = 3.6$, $P < 0.001$), or by *Hypsipetes philippinus* (paired t-test: $t_{54} = 7.7$, $P < 0.001$). The unexpectedly low visitation rates of 'Lunok b' have already been mentioned (see Methods).

Statistical differences among the non-Moraceae could only be demonstrated with respect to *Platea excelsa* (Fisher's least significant difference procedure, $P < 0.5$), in which no disperser species was recorded during any observation period. An exception is the small-fruited and sparsely-seeded *Schefflera octophyllum*. Visitation rate at this species is not only significantly higher than those at all large-fruited plants (Fisher's least significant difference procedure, $P < 0.5$), but also than those of the other members of the same size class. Furthermore, it attracted more visitors per hour than the figs *Ficus irisan*a and both 'Lunok' trees.

DISCUSSION AND CONCLUSIONS

Comparison across plant taxa. The results presented in this study reflect the relative success of individual plants in attracting dispersers. The importance of fruits to the birds may be dependent on what other species are fruiting simultaneously, because frugivores are known to select among fruits according to crop size (Howe & Estabrook 1977), high pulp-to-seed ratio (Herrera 1981a), seed size (Sørensen 1984), pulp mass (Johnson *et al.* 1985), sugar concentration (Levey 1987a), fruit size (Moermond & Denslow 1983), and ease of harvest (Moermond & Denslow 1983). Our work confirmed the high attractiveness of figs for avian frugivores documented in other studies (e.g., Janzen 1979, Snow 1981, Stiles & Rosselli 1993, Athreya 1997). This could be demonstrated by both the high visitation rates by fruit-eating birds (Fig. 4) and the high diversity of frugivorous bird species visiting fig trees (Fig. 3). The large size of 'Lunok a'-fruits (Moraceae) relative to other fig species, or the larger size of 'Dalakit' fruits relative to smaller

non-Moraceae fruits, have apparently no negative effect on numbers of disperser species, since the soft flesh can be penetrated by the bills of birds unable to swallow the fruit whole.

The fig trees in this study had short and peaked fruiting periods accompanied by strong within-crown synchrony of fruit ripening, thus increasing the mean proportion of fruits available per day and providing a bountiful supply of sugar-rich fruits (Lambert & Marshall 1991). The non-Moraceae tree species (except *Schefflera octophyllum*) provided smaller crops relative to *Ficus* (pers. judgement), and even when they had large crops the proportion of ripe fruit at any one time was low. In addition, small-gaped birds such as the Dicaeidae and *Zosterops* can only eat from

fruits larger than their gape if they are soft enough to be broken piecemeal while still attached to the tree. Soft-skinned figs are unusual in that most can be harvested by smaller birds, irrespective of fig size (Lambert & Marshall 1991). The relatively low visitation rate at *Ficus irisanana* possibly relates to its growth form. Whereas all other Moraceae species under study were strangler figs and formed components of the highest forest strata, *Ficus irisanana* was a tree of the midstory with a much less extensive canopy and thus smaller crop size. Therefore *Ficus irisanana* trees might be more difficult to locate by avian frugivores, and their smaller crop sizes make them less attractive.

Regarding visitation rates, differences among the non-Moraceae species were not marked. The large

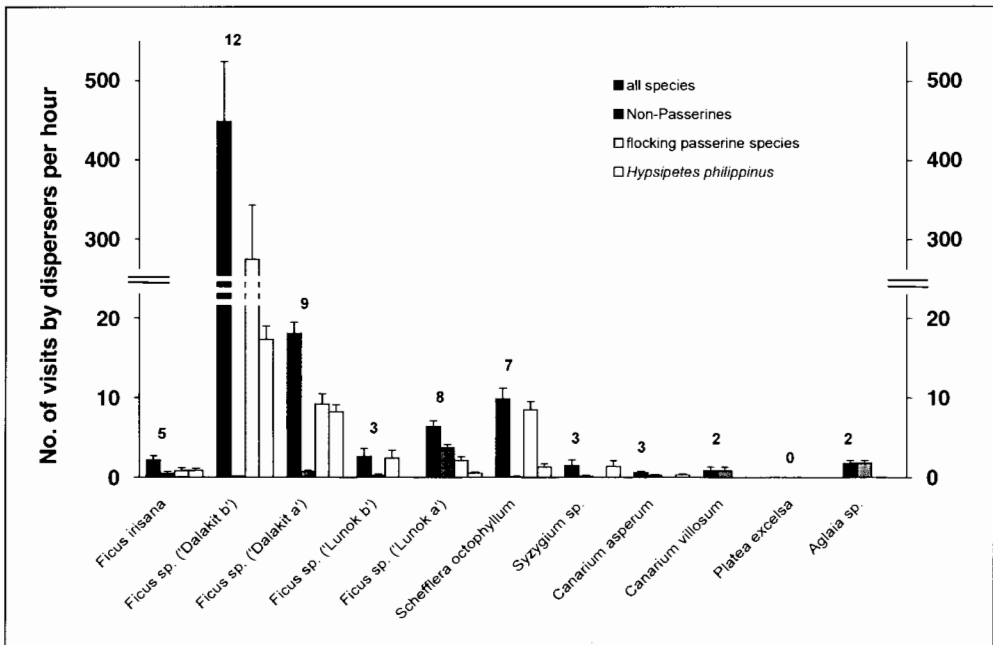


FIG. 4. Mean numbers of visits by avian dispersers to each of the plant species listed. Error bars are standard errors. For total number of observation hours per tree see Table 1. Numbers above bars are total number of species seen visiting during observation periods. Mean values of the following bird species groups are shown separately: on-passerines: Columbidae, *Loriculus philippinus*, *Megalaima haemacephala*; flocking passerine species: passerines which were often recorded in fast-moving mixed and/or single-species flocks (Rhabdornithidae, Dicaeidae, *Zosteropidae*, *Eumyias panayensis*); *Hypsipetes philippinus*: this species was regularly recorded in monospecific flocks, but often stayed near the focal plant. Plant species with low numbers of observation hours and unfavorable observation conditions were omitted from the analysis. The visitation rate for *Platea excelsa* was 0, since the only potential disperser species recorded (*Ducula poliocephala*, see Table 2) was observed outside the observation periods.

fruit and seed sizes of *Aglaia* sp., *Platea excelsa*, and *Canarium villosum* excluded the majority of the frugivorous birds in the NNFR because they exceeded the gape size of most species. Fruit pigeons and hornbills occur at lower densities (and feed in smaller groups) than the smaller passerines which may explain the low visitation rates at the large-fruited trees. No avian disperser species was ever recorded in *Platea excelsa* during observations. *Platea excelsa* was a relatively common tree species within the study area with many individuals fruiting simultaneously. This diminished the chance of an observer witnessing a visit by a disperser species at a focal tree. The fruit pigeon *Ducula poliocephala* was only incidentally observed in *Platea excelsa* trees when one of us (M. H.) walked along the trails to or from the plants under study.

The low visitation rates at non-Moraceae species with fruit sizes below 15 mm may be explained by the high seed-to-pulp mass ratio which makes them less attractive for birds due to gut loading imposed by the seeds (Herrera 1981b). An exception was *Schefflera octophyllum*. Its fruits exhibited a fig-like high pulp-to-seed ratio and were densely packed in racemes so that a frugivore could take many fruits without changing its position. This circumstance, and the small fruit size, might render *Schefflera octophyllum* more attractive for a wider array of avian frugivores than all other non-Moraceae and some Moraceae species. But it has to be noted that the observed *Schefflera octophyllum* individual was mainly exploited by a group of six to ten *Dicaeum trigonostigma*, which stayed in the plant's vicinity and entered it frequently. This would partly explain the high visitation rates of dispersers per unit of time for this species.

The distinction between 'good' and 'bad' dispersers – is it useful? The recorded fruit-handling techniques displayed by the avian frugivores in this study classify them all as potential dispersers for the plant species under scrutiny. The birds either swallowed fruits whole with or without prior handling, or they took bits of pulp from those fruits with many tiny seeds, so that even small pieces should contain at least some seeds for dispersal. The only explicit cases of fruit theft were observed during the use of *Platea excelsa* by *Zosterops montanus*, when parts of the pulp were eaten while leaving the large seed on the tree, thus exposing the fruit to insect or microbe attack and desiccation.

Data on seeds being destroyed by handling or digestion are not available. *Loriculus philippensis* is

commonly known to ingest pulp and juice of fig fruits (species account in "Handbook of the Birds of the World", Vol. 4, 1997). However, it may also crush and digest seeds as is habitual for the Psittacidae (Collar 1997). The gizzard walls of fruit pigeons of the genera *Ptilinopus* and *Ducula* are endowed with hard ridges, nodules, and in *Ducula* even with tooth-like structures (Garrod 1874, Cadow 1933). These grinding plates rub the fleshy pulp and skin off the fruit; the seeds pass through the intestine undigested and are expelled whole (Baptista *et al.* 1997). Whether they are able to germinate after this treatment still remains to be tested. But the gizzards of *Ptilinopus* and *Ducula* do not contain the seed-crushing gastroliths found in more granivorous species like *Phapitreron leucotis* (Baptista *et al.* 1997).

The duration of a visit at a tree determines whether a bird is likely to disperse swallowed seeds or deposit them beneath the parent tree. Generally, the non-passerines of this study stayed longer in the food plants than the passerines, which does not favor their role as seed dispersers. Especially the obligate frugivores, like the fruit pigeons (Ptilinopodinae) and the barbet *Megalaima haemacephala*, were observed to stay in a tree for hours, often resting, probably for digestion. Conversely, the short duration of visits by passerines implies that they often left the feeding tree before they defecated or regurgitated the ingested seeds. Especially those species normally not regarded as frugivores (*Zosterops montanus*, *Eumyias panayensis*) generally stayed less than 10 min. Pratt & Stiles (1983) found similar results in Papua New Guinea frugivores and part-time frugivores. It is evident that visit length becomes a clue to the dispersal quality of the given bird species only when it is related to the time period a bird needs to expel the ingested seed. Several studies have demonstrated that small seeds are retained longer in the gut than larger or regurgitated ones, and might therefore travel farther from the parent plant (Sørensen 1984, Johnson *et al.* 1985, Levey & Grajal 1991). Therefore with regard to visit length a given bird is not inherently a good or poor disperser (Levey 1987b), since the resultant seed shadow may depend on fruit traits, seed size, and the bird's favored mode of seed ballast elimination (Johnson *et al.* 1985).

There is evidence that in order to minimize the problem of a limited gut volume, and to meet their nutritional requirements, the digestive system of highly frugivorous birds is adapted to rapid fruit processing,

thus resulting in short gut-transit times and high regurgitation rates (Johnson *et al.* 1985, Levey 1986, Worthington 1989, Karasov & Levey 1990). Fruit pigeons of the genera *Ducula* and *Ptilinopus* have short and wide guts, allowing them to process bulky fruits fairly quickly (Cadow 1933, Bowman 1994), whereas for the partially frugivorous *Dicaeum hirundinaceum* and *Zosterops lateralis* Keast (1958) reports passage times for mistletoe seeds of 25–60 min and 30–80 min, respectively; *Hypsipetes philippinus* was found to process seeds of nine tree species in 8 to 27 min (arithmetic means, Schabacker 1998). If these data can be extrapolated to the observed visit lengths in this study, then the chance of chiefly frugivorous birds depositing seeds below the parent tree is higher than for the partially frugivorous passerines.

Distances traveled after birds leave fruiting plants could not be determined. Fruit pigeons (*Ptilinopus occipitalis*, *Ducula poliocephala*) and Philippine Bulbuls (*Hypsipetes philippinus*) often seemed to stay in the closer vicinity of the feeding tree in order to make repeat visits. Conversely, it is to be expected that typical insectivores (*Zosteropidae*, *Eumyias panayensis*) and members of mixed-species flocks (*Rhabdornithidae*, *Dicaeidae*, *Eumyias panayensis*, *Zosterops montanus*) or of large monospecific flocks (*Zosterops montanus*) travel longer distances, thus carrying seeds away from parent trees before depositing them. For insectivores, fruits might be a cheap snack which they take on their way to localities where insects are more abundant, e.g., especially at the edges of treefall gaps (Hovestadt, pers. comm.).

Given the inaccuracies of the present study due to difficult observation conditions, one can be tentatively concluded that the typical frugivores tend to be poorer dispersers than passerines since they exploit fruiting trees in long visits (*Ptilinopodinae*, *Megalaima haemacephala*) or make repeated visits from nearby, whereas the passerine insectivores, and members of mixed and/or conspecific flocks, travel fast and far to carry seeds away from the parent tree, eventually depositing them at more appropriate germination sites. Furthermore, there is evidence (Lambert 1989, Collar 1997, Baptista *et al.* 1997) that members of the *Psittacidae* (but see Böhning-Gaese *et al.* 1995) and *Columbidae* may harm or even destroy seeds while processing fruits. Hence these groups may be poorer dispersers for an additional reason.

Effects of fruit size – how strong is the ecological interdependence between plant and frugivore? Our study provides evidence (see Fig. 3 and Table 2) that small-fruited plants or plants with soft fruits and many tiny seeds (figs) attracted a wide spectrum of frugivorous bird species, mainly of small body size, that complement their diet with arthropods. By contrast, large-fruited and generally large-seeded plants are dispersed by only a few large and obligately frugivorous birds (see Hamann & Curio 1999). In this respect, our results reflect the same relationship between avian frugivores and tropical trees with their associated characters as was postulated in Howe & Estabrook's (1977) and Howe & Smallwood's (1982) paradigm on specialized and generalized systems in bird-plant interactions. However, the paradigm further assumes that for large-fruited plants seed dispersal to appropriate sites of germination is critical for their recruitment, whereas for small-fruited plants seed dispersal may not be that critical, since many seeds may remain dormant. Thus the paradigm implies that there is an association of plant/frugivore characters with specific and strong ecological interdependencies between specialized seed-dispersing frugivores and their large-fruited food plants.

It is evident that large fruit size limits the spectrum of potential disperser species to birds with large gape sizes. This could be demonstrated quantitatively within the *Moraceae*, where the large-fruited fig species 'Lunok a' was mainly exploited by large-gaped non-passerines (*Ptilinopodinae*, *Megalaima haemacephala*), and qualitatively at *Aglaia* sp., where the fruit pigeon *Ptilinopus occipitalis* was observed unsuccessfully trying to swallow an *Aglaia* seed, whereas the larger *Ducula poliocephala* was able to ingest more than five of them within less than half a minute. Thus, in this study maximum fruit size is constrained by frugivore gape size. However, our results are not consistent with the notion of specialized dispersal systems, since the large frugivores displayed poorer dispersal behavior than the smaller facultatively frugivorous species. Rather, our study suggests that plant species for which dispersal is essential for seedling recruitment should rely on smaller non-specialized bird species and hence should produce small fruits matching their gape sizes. Furthermore, there is evidence that dispersal efficiency decreases with increasing seed size since birds void larger seeds more rapidly by regurgitation (Sørensen 1984, Johnson *et al.* 1985), or pass them

more quickly through the gut (Levey & Grajal 1991, Schabacker 1998). Finally, plant species with large and nutrient-rich seeds tend to be adapted to germination in shaded sites (Geritz *et al.* 1984, Foster & Janson 1985). This implies selective benefits for small seed size in dispersal-dependent plant species (Courtney & Sallabanks 1992), whereas in large-seeded plants seed size is not predominantly selected for by frugivores but by the abiotic and/or biotic conditions after dispersal, thus making dispersal not strictly necessary for the establishment of seedlings (but dispersal still should pay for plants suffering inbreeding depression, Gibson & Wheelwright 1995, and because of escape benefits, see Introduction). Conversely, seed mortality in the rainforest seed bank is probably very high (Hovestadt, pers. comm.), so that seed dispersal of small-seeded plants to appropriate sites (e.g., treefall gaps), where seeds can germinate soon after deposition, may be more essential for recruitment than for large-seeded species. However, small-fruited plants are exploited opportunistically by a large spectrum of unspecialized frugivores, so that it is difficult to describe this relationship as specialized.

Up to now perhaps the most extreme examples of specialized interactions between a fruiting plant and its avian seed dispersers have been demonstrated between mistletoes and their consumers (in the Old World and Australasian Dicaeidae and Meliphagidae; Reid 1989, 1991), and between Central European oak trees and the Eurasian jay, *Garrulus glandarius* (Bossema 1979). Particularly the bird-mistletoe interaction shows that a specialized system can involve small birds and small-fruited plants, and that specializations in fruit-bird interactions are not necessarily determined by the large size of fruits and their consumers.

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