NOTES ON FRUIT CONSUMPTION OF THE PHILIPPINE BULBUL(*Hypsipetes philippinus*) AND ITS QUALITY AS A SEED DISPERSER

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ABSTRACT

*The Philippine Bulbul (*Hypsipetes philippinus, Pycnonotidae*) is, by virtue of its relative abundance, the most common frugivorous bird in primary and secondary forests in the West Visayas, Philippines. This paper compiles data on 49 tree species used for their fleshy fruits by the Philippine Bulbul. Additional more detailed observations were made on one tree each of four fig (*Ficus sp.*) species as well as a number of other fruit-eating forest birds.*

Bulbuls feed in general on small fruits of up to 20 mm in diameter. Depending on tree species, they eat 66-82% of the fruits which they pluck from the source tree and drop only a minor proportion into the ground. Only less than 9-22% of fruits harvested are carried away from the source tree in the bird's beak. Since birds stay in the near vicinity of an exploited tree, the fraction of fruits carried over long distances seems to be small. However, of those many seeds ingested on and near a source tree, a substantial fraction may be dispersed over longer distances upon passing the gut. The bulbul benefits a fruiting tree through seed dispersal since it ingests all seeds by swallowing the fruits whole. Both this species and other frugivorous birds handle (eat, drop, carry) fruits in distinct ways irrespective of the tree species on which they feed. Thus, birds of up to eight species, including the bulbul, exploiting the same fig species differ significantly from each other in the manner of handling mentioned. This translates into quality differences among those birds as seed dispersal agents. Being a generalist frugivore, and because of its abundance, the Philippine Bulbul may be among the most important seed dispersers in this region. Other forest birds, though being in part more specialized on fruits, appear to rank lower as seed dispersers for a number of reasons.

Introduction

In tropical rainforest about 60–90% of the plants are adapted to disperse their seeds with the help of vertebrates (Fleming 1979, Howe & Smallwood 1982, Dirzo & Domínguez 1986, Hamann & Curio 1999, Hamann et al. 1999). Woody plants of the understory in particular depend on animal mediated seed dispersal (Howe & Smallwood 1982, Howe & Westley 1988). Along with various species of mammals (van der Pijl 1972, Fleming 1981, 1986, Cox et al. 1991, Bizerril & Raw 1997, Whitmore, T. C. 1991), birds are among the most important seed dispersal agents in tropical forests (van der Pijl 1972, Stiles 1980, Howe & Smallwood 1982, Corlett 1998a). This characteristic of birds affects plant species composition (Janzen 1970) and may be so important that a given species may qualify as a keystone species (Cox et al. 1991, Powers et al.1996). Hence, in tropical biology, seed dispersal by frugivorous animals takes center stage.

To gain further insight into the mutualistic interactions between fruiting plants and frugivorous animals in a given area, basic studies are still needed. This study focuses on the Philippine Bulbul (*Hypsipetes philippinus*, Pycnonotidae) in order to identify the fruiting trees it uses for food, and to establish both its quality and its efficiency as a seed dispersing agent in the West Visayas, Philippines.

The endemic Philippine Bulbul is one of the most common frugivores in the Philippines. The bird is the size of a thrush and rather inconspicuous when skulking in foliage. The sexes are alike (Kennedy et al. 2000). Distributed from sea level up to about 2,000 m a.s.l., it can be found in primary and secondary forests, in mangrove and lowland rainforest, as well as mountain mossy forest (Dickinson et al. 1991, Kennedy et al. 2000). It lives regularly along the edges of clearings and cultivated areas close to original forests, as well as in patches of secondary growth (Rabor 1986). Being highly social, it roams the woods in groups or in mixed species flocks. Breeding occurs from March to July (Dickinson et al. 1991). The bird is known to feed on fruits as well as insects (Rabor 1986).

Material and Methods

Study areas and birds

Observations at fruiting trees were conducted at the research station of the Philippine Endemic Species Conservation Project (PESCP) on the island of Negros, Philippines. The study site is situated in the North Negros Forest Reserve (NNFR) within the jurisdiction of the province of Negros Occidental. This forest reserve lies between the volcanoes Mt. Silay (1,510m) and Mt. Mandalagan (1,885m), and is about 80,454 ha. Both secondary forest (1/3) and primary forest (2/3, Diestel 1996) cover about 20% (16,487ha) of the area. Observations were conducted near the village of Patag, Silay City district (10°41.7'N; 123°10.6'E; 650m a.s.l.) on the NW slope of Mt. Mandalagan between 23 August and 10 September 1996 (see also Heindl & Curio 2000, Hamann & Curio 1999).

Additional capture of Philippine Bulbuls and further observations on their fruit consumption were carried out at the PESCP research station at Sibaliw in the NW of Panay island (11°49.2'N, 121°58.1'E) during the summer and winter 1997/98. Situated about 450m a.s.l., the station is located within a former farmland (kaingin) surrounded by primary forest. Parts of the kaingin fields are now stocked by 25 year old secondary forest. Birds were netted in mist nets which were placed mainly in the former kaingin fields and at the edges of the nearby primary forest. The following morphological data were taken: body weight, body length, wing length, tail length, beak length, beak width at base.

Located less than 190 km from each other, both research areas belong to the West Visayan biogeographic region. Hence, for the most part they are comparable in forest composition and other biotic and abiotic factors such as the weather.

Observations at fruiting trees

Four fruiting fig trees (*Ficus* sp., Moraceae) were observed for 1–5 days near the village of Patag in the NNFR. Observations went on from early morning until rain started in the afternoon. The visiting bird species and their behavior were recorded. Individuals were observed for as long as it was possible to do so until they disappeared in the foliage.

Fruit handling by birds is divided into three categories: 1. Fruits eaten; 2. Fruits dropped from the tree; 3. Handling of fruits with unknown outcome. This latter category includes an unknown proportion of fruits carried off in the bird's beak. No estimate can be made in terms of distance or quantity of the fruits dispersed by being carried off in the bird's bill. Because of the dense canopy, the data are biased in favor of the more abundant and the more active bird species. Hence, no estimate of the relative abundance of a bird species at a given fruiting tree could be made.

On Panay, only the visiting birds and the species of tree they visited were recorded. In order to establish the full range of fruits used by the Philippine Bulbul, all seasonally available fruiting trees were observed during mornings between 6 and 12 o'clock until at least several bulbuls had eaten fruits of a tree under scrutiny. The array of fruits consumed by the bulbul was further estimated by examining the faeces of caught birds. In some cases direct observation could not verify an particular fruit species that the birds readily took in the cage even though fruits known to be used by the bulbul in the wild were present as well. From this observation, it is possible to regard those fruits as being part of the food in the wild, too.

Statistics

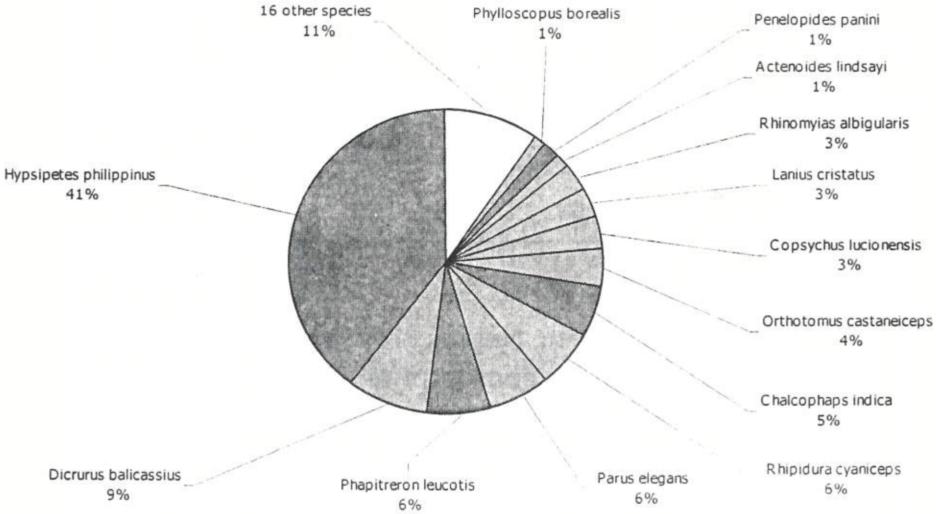
Tests were run with the SPSS 10.0.7 package; p values are given two-tailed.

Results

Avifauna of West Visayan forests

Out of 271 bird species listed for Negros by Dickinson et al. (1991), 111 have been recorded by project members during the years of study within the NNFR. Out of the 111 observed, 85 occur in forest habitats. According to our observations as well as information from locals, 36% of these species are known to feed on fruit. They include 8 doves, 4 parrots, 2 hornbills, 2 bulbuls, all belonging to families of mainly fruit-eating birds. Others like 2 *Rhabdornis*, 2 orioles, and 1 starling have also been observed feeding in many fruiting trees, and maybe considered potentially important for seed dispersal (see Hamann & Curio 1999, Heindl & Curio 2000 for species names).

Fig. 1: Forest birds netted on Panay, broken down to species. Total = 267. Frugivorous species in dark gray. The others are mixed-diet feeders or insectivorous.



By virtue of its relative abundance, the Philippine Bulbul is one of the most common frugivorous birds in primary and secondary forest in this area. About 41% of the caught birds were bulbuls (Fig. 1). Other fruit eating birds like the fruit doves *Phapitreron leucotis* (6%), or Hornbills *Penelopides panini* (1%), were much less abundant. The netting data reflect the abundance of frugivores in secondary forest and at the edges of primary forest. However, estimating the relative abundance from capture data might be biased because of two reasons. First, birds differ in the probability of being caught in mist nets; second, the netting covers only the lower 15 m above ground. This includes all strata in the secondary forest but primary forest is usually much taller. Though the true relative abundance of species other than the bulbul might be higher, the bulbul is still the most abundant frugivorous bird in this area. Morphological data of *Hypsipetes philippinus* given in Table 1 show the size of the bird and its bill size (beak width at base=gape size).

Table 1: Morphological data of 107 *Hypsipetes philippinus (guimarasensis?)* on Panay Island.

	Body weight [g]	Body length [mm]	Wing length [mm]	Tail length [mm]	Beak length [mm]	Beak width at base [mm]
Arithmetic-mean	47.4	222.4	104.5	83.8	22.6	13.
± s.d.	3.8	36.4	5.2	14.3	2.6	1.

Fruit consumption

The fieldwork on Negros (1996) and Panay (1997 and 1998) revealed the consumption of fruits of 25 tree species by bulbuls as judged from direct observation and/ or from seeds in the faeces (Table 2). Two species are known through their seeds only. For four additional fruit species the direct evidence for consumption in the wild is missing although the birds took these fruits readily in the cage in the presence of established food-fruits. Data from Hamann & Curio (1999) reveal the use of 10 fruit species while Heindl & Curio (2000) reported 10 more additional fruit species. Taken together the data reveal the use of 49 fruiting tree species by the bulbul (Table 2). Among these, Euphorbiaceae (9 species) and figs (Moraceae) (up to 13 species) are the bulk of all species consumed.

Table 2: Fruits consumed by bulbuls as judged from direct observation (o) or from seeds in the feces (s); measurements viz. counts: arithmetic mean ± s.d. For four fruit species the observation of consumption in the wild is missing but the birds took these fruits readily in the cage in the presence of established food-fruits (c). Observation on p = Panay, n = Negros. Indet = unidentified tree species. Data from hm = Hamann & Curio 1999 and hdl = Heindl & Curio 2000, both on Negros, included.

	Scientific name	Family		Fruit height length?	Fruit width	Number of seeds	Seed height length?	Seed width
1	*indet. 1.*	-	o/p	-	-	-	-	
2	*indet. 2.*	-	s/p	-	-	-	16.2 (n = 1)	12.0 (n = 1)
3	*indet. 3.*	-	s/p	-	-	-	5.4 (n = 1)	2.5 (n = 1)
4	*Schefflera octophyllum*	Araliaceae	hdl		3-4 (estimate)	some		< 1 (estimate)
5	*Polyscias nodosa Wall.*	Araliaceae	o/p	5.8 ± 0.5 (n = 20)	7.2 ± 0.3 (n = 20)	5 (estimate)	3.4 ± 0.1 (n = 10)	2.5 ± 0.1 (n = 10)
6	*Canarium asperum*	Burseraceae	hdl		12.3 ± 0.9 (n = 25)	1 (estimate)		11.5 ± 0.9 (n = 4)
7	*Elaeocarpus sp.*	Elaeocarpaceae	hdl	-	7.9 ± 0.7 (n = 9)	1 (estimate)	-	5.5 ± 0 (n = 2
8	*Elaeocarpus cf. multiflorus (Poir.) Muell.-Arg.*	Elaeocarpaceae	o/p	10.2 ± 0.6	7.2 ± 0.3 (n = 20)	1 (estimate)	8.9 ± 1.1	5.3 ± 0.6 (n = 20)

Table 2 (continued)

	Scientific name	Family		Fruit height length?	Fruit width	Number of seeds	Seed height length?	Seed width
9	*Macaranga tanarius (L) M.A.*	Euphorbiaceae	hm	10	-	-	3	-
10	*Macaranga bicolor Muell.-Arg.*	Euphorbiaceae	o/p	-	-	1	-	-
11	*Bischhofia javanica Bl.*	Euphorbiaceae	hm	11	-	-	4	-
12	*Homalanthus alpinus Elm.*	Euphorbiaceae	hm	10	-	-	5	-
13	*Antidesma pleuricum Tul.*	Euphorbiaceae	o/p	4.4 ± 0.2	4.2 ± 0.2 (n = 20)	1 (estimate)	3.7 ± 0.2 (n = 19)	1.7 ± 0.1 (n = 19)
14	*Breynia cf. rhamnoides (Retz) Muell.-Arg.*	Euphorbiaceae	o/p	5	4 (estimate)	6 (estimate)	2 (estimate)	1 (estimate)
15	*Aporosa aurita (Tul.) Merr.*	Euphorbiaceae	o/p	9.4 ± 0.2 (n = 14)	8.6 ± 0.4 (n = 14)	2 (estimate)	8.1 ± 0.2	7.8 ± 0.4 (n = 8)
16	*Neoscortechinia philippinensis (Merr.) Welzen*	Euphorbiaceae	o/p	19.2 ± 1.0	11.3 ± 0.6	1	17.2 ± 1.2 (n = 20)	11.7 ± 1.7 (n = 20)
17	*Mallotus mollissima (Geisel) A. Shaw*	Euporbiaceae	hm	10	-	-	3	-

18	*Cinnamomum sp.*	Lauraceae	o/p	16.1 ± 1.6 (n = 19)	12.0 ± 0.1 (n = 19)	1	14.5 ± 1.1 (n = 19)	10.7 ± 0.8 (n = 19)
19	*Leea aculeata Blume*	Leeaceae	o/p	9.8 ± 0.4	14.0 ± 0.8	5.1 ± 2	6.2 ± 0.3 (n = 20)	5.1 ± 0.3 (n = 20)
20	*indet. 4.*	Meliaceae	c/p	14.1 ± 0.6 (n = 30)	10.9 ± 0.5	1	11.7 ± 0.5 (n = 30)	8.1 ± 0.5 (n = 30)
21	*Ficus heteropleura*	Moraceae	hm	10	-	-	1	-
22	*Strebus glaba (Merr.) Corner*	Moraceae	hm	-	-	-	-	-
23	*Ficus irisana*	Moraceae	hdl	-	6.6 ± 0.5	many	-	< 1 (estimate)
24	*Ficus benjamina*	Moraceae	o/p	16.9 ± 3.2	12.6 ± 1.9	many	-	-
25	*Ficus chrysolepis*	Moraceae	o/n	23.6 ± 8.1 (n = 10	21.8 ± 1.1 (n = 10)	many	-	-
26	*Ficus sp. 1*	Moraceae	o/p	10.9 ± 2.6 (n =20)	9.8 ± 1.5 (n = 20)	many	-	-
27	*Ficus sp. 2*	Moraceae	o/n	13.3 ± 1.0 (n = 12)	14.8 ± 0.4	many	-	-
28	*Ficus sp. 3*	Moraceae	o/n	9.0 ± 0.8 (n = 20)	8.7 ± 0.8	many	-	-

Table 2 (continued)

	Scientific name	Family		Fruit height length?	Fruit width	Number of seeds	Seed height length?	Seed width
29	*Ficus sp. 4*	Moraceae	o/n	19.7 ± 1.2 (n = 17)	23.7 ± 1.3 (n = 17)	many	-	-
30	*Ficus sp. 5*	Moraceae	hdl	-	11.2 ± 0,7 (n = 10)	many	-	< 1 (estimate)
31	*Ficus sp. 6*	Moraceae	hdl	-	10.5 ± 0.7 (n = 18)	many	-	< 1 (estimate)
32	*Ficus sp. 7*	Moraceae	hdl	-	10.5 ± 1.1 (n = 23)	many	-	< 1 (estimate)
33	*Ficus sp. 8*	Moraceae	hdl	-	19.4 ± 2.7 (n = 17)	many	-	<1 (estimate)
34	*Ardisia sp.*	Myrsiniaceae	c/p	6.6 ± 0.4 (n = 20)	7.6 ± 0.5	1	5.39 ± 0.3	5.1 ± 0.3 (n = 20)
35	*Syzygium sp. 1*	Myrtaceae	hm	22	-	-	11	-
36	*Syzygium sp. 2*	Myrtaceae	hm	23	-	-	10	-
37	*Syzygium sp. 3*	Myrtaceae	o/p	10.9 ± 0.2 (n = 20)	13.0 ± 0.1 (n = 20)	1 (estimate)	8.9 ± 0.1	7.9 ± 0.5 (n = 20)
38	*Syzygium sp. 4*	Myrtaceae	hdl	-	6.6 ± 0.9	1 (estimate)		6.3 ± 1.1 (n = 2)

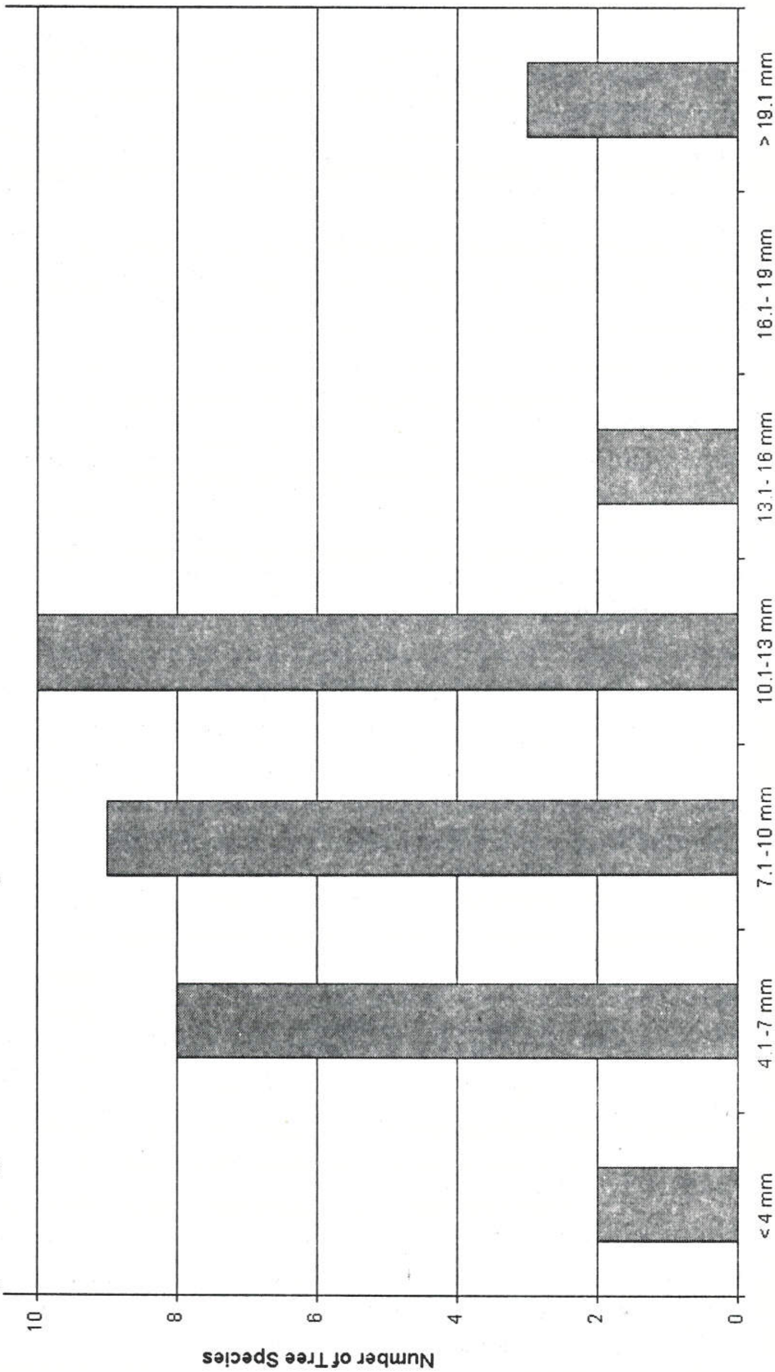
39	*Decaspermum cf. fruticosum Forst*	Myrtaceae	o/p	5.1 ± 0.4	6.6 ± 0.7 (n = 20)	20 (estimate)	2 (estimate)	1
40	*Pandanus sp.*	Pandanaceae	hdl	-	4-5 (estimate)	some	-	< 1 (estimate)
41	*Gynotroches axillaris Blume*	Rhizophoracea	o/p	5.1 ± 0.6 (n = 20)	5.1 ± 0.5 (n = 20)	18.0 ± 3 (n = 44)	1.5	1
42	*Lasianthus cf. morus Elm.*	Rubiaceae	c/p	13.2 ± 1.7	11.2 ± 1.0	4.2 ± 1	5.2 ± 0.5	2.3 ± 0.3 (n = 20)
43	*indet. 5. (Psychotria ?)*	Rubiaceae	c/p	10.7 ± 0.9	8.9 ± 0.8 (n = 20)	2 (estimate)	8.2 ± 0.4 (n = 20)	5.6 ± 0.3 (n = 20)
44	*Guioa pleuropteris*	Sapindaceae	hm	15	-	-	3	-
45	*Eurya sp.*	Theaceae	o/p	3.9 ± 0.6	5.1 ± 0.8 (n = 20)	16.0 ± 4 (n = 50)	1 (estimate)	1
46	*Wikstroemia cf. ovata C.A. Mey*	Thymelieaceae	o/p	9.2 ± 0.5 (n = 20)	9.3 ± 0.6 (n = 20)	1	6.4 ± 0.4 (n = 20)	6.8 ± 0.9 (n = 20)
47	*Grewia multiflora*	Tiliaceae	hm	17	-	-	4	-
48	*Lantana camara Lin.*	Verbenaceae	o/p	-	-	1 (estimate)	-	-
49	*Geunsia cumingiana Rolfe*	Verbenaceae	o/p	4.6 ± 0.4 (n = 20)	6.8 ± 0.7 (n = 20)	10 (estimate)	3.1 ± 0.3	1.9 ± 0.2 (n = 17)

In general *Hypsipetes philippinus* arrive at a fruiting tree in flocks of various sizes. Only from time to time could solitary individuals or pairs be observed. Larger flocks contained more than 15 individuals. Birds pluck part of the fruits while perched on a branch. In most cases, however, bulbuls feed on the wing, plucking a fruit while hovering or jumping, or during a short flight. Carrying the fruit in its beak, a bird flies to a nearby branch and perches there to feed on it. Often birds fly longer distances with the fruit in their beaks and disappear in the surrounding trees.

Observations during fieldwork indicate that bulbuls fed on small fruits of about 10 mm in diameter (Fig. 2). They were not seen on trees with very large fruits and they generally did not peck at fruits to eat only the pulp. The length of the fruits ranged from 3.9±0.6mm to 19.2±1.0mm, the width from 4.2±0.2mm to 14.8±0.4mm. However, soft figs were as large as 19.7±1.2mm in length and 23.7±1.3mm in width (Table 2). The bulbuls usually selected the smaller ones from the range of fruits offered on this trees. With fruits of this size, however, the birds had obvious difficulty swallowing them. Birds pecked at soft fruits that exceeded 20mm diameter in width and swallowed only bits of pulp (Table 3). However, this was only observed on fig trees on Negros. Exceptionally, the fruits of one tiliaceaous tree (*Microcos stylocarpus*), although within the size range of consumed fruits (Fig. 2), were not taken by the birds, neither during the 20h of tree observation, nor in captivity. Likewise this tree was not visited by any other bird species in the same time.

Seeds are in general not regurgitated by the bulbul but defecated, and remain intact even after a gut passage time of between 5 and 51 min, with a median of 14 min ($Q_{25\%}$=11min, $Q_{75\%}$=21 min, n=47) (Schabacker & Curio 2000). 57 fecal samples were found and examined in the bags used to transport the birds. Out of these fecal samples, 16% contained parts of insects like antennaes, wings, or legs.

Fig. 2: Frequency distribution of the maximum width of the fruits consumed by the Philippine Bulbul on Panay and Negros. Total = 34 fruit species. See also Table 2.



A close look at four fig species revealed that the bulk (weighted mean 78%, n=323) of the fruits handled by birds of all species observed on the four trees were eaten (Table 3–6). Only about 13% (weighted mean) were dropped in the process, usually accidentally. Nine per cent (0–14%) of the fruits were handled while the bird was hidden from the observer. Because fruits 'handled unseen' could have been eaten further away from the parent tree, the proportion of fruits dispersed from the bird's bill and hence dropped without gut passage must be lower than 9%. This means also that the percentage eaten was certainly larger than 78%. Bulbuls do not differ from this overall picture. They ate at least 66–82% and dropped maximally 5–11% of the fruits they had plucked. Fruit doves and Hanging Parrots wasted more fruits of *Ficus chrysolepis* (Table 3). Bulbuls often plucked fruits on the wing and then flew some distance to a perch, as described above. Therefore, 9–22% of the fruits were handled while the bird was hidden from the observer. In general, the bulbuls tended to stay in the near vicinity of the parent tree and soon returned to it after finishing the fruit they had taken along. Flowerpeckers (*Dicaeum* spp.), Coletos (*Sarcops calvus*), and White-eared Brown-dove *Phapitreron leucotis* also carried away some fruits in their bill (Table 3–5). Because of their small size, flowerpeckers eat only parts of the pulp which may not contain large numbers of seeds.

Table 3 (on the right): Bird species feeding on *Ficus chrysolepis* Miq. (Moraceae). 25 Aug. – 1 Sep. 1996. Red fruits: height 23.6 ± 8.1 mm, range 22.3 – 31.0 mm; width 21.8 ± 1.1 mm, range 19.8 – 22.9 mm; weight 6.5 ± 1.1 g, range 4.5 – 7.6 g; n = 10.

Table 4 (right): Bird species feeding on *Ficus* sp. 2. (Moraceae). 1 – 9 Sep. 1996. Soft red fruits: height 13.3 ± 1.0 mm, range 12.3 – 15.3 mm; width 14.8 ± 0.4 mm, range 13.9 – 15.2 mm; weight 1.6 ± 0.2 g, range 1.4 – 2.0 g; n = 12.

Table 3.

Bird species	Feeding on	Fruits eaten where plucked (n)	Fruits dropped (n)	Fruits handled unseen (n)	n
Dicaeum bicolor	fruit parts	88% (15)	12% (2)	-	17
Ducula poliocephala	fruits, whole	64% (15)	36% (6)	-	21
Hypsipetes philippinus	fruits and fruit parts	82% (9)	9% (1)	9% (1)	11
Loriculus philippensis	fruit parts	73% (35)	27% (13)	-	48
Megalaima haemacephala	fruit parts	86% (6)	14% (1)	-	7
Ptilinopus occipitalis	fruits, whole	77% (14)	22% (4)	-	18
Sarcops calvus	fruit parts	50% (1)	-	50% (1)	2
Total		77% (95)	22% (27)	2% (2)	124

Table 4.

Bird species	Feeding on	Fruits eaten where plucked (n)	Fruits dropped (n)	Fruits handled unseen (n)	n
Dicaeum bicolor	fruit parts	63% (26)	20% (8)	17% (7)	41
Dicaeum trigonostigma	fruit parts	89% (8)	-	11% (1)	9
Hypsipetes philippinus	fruits and fruits parts	74% (56)	5% (4)	21% (16)	76
Megalaima haemacephala	fruit parts	100% (1)	-	-	1
Oriolus chinensis	fruit, whole	100% (1)	-	-	1
Phapitreron leucotis	fruit, whole	96% (25)	-	4% (1)	26
Ptilinopus occipitalis	fruit, whole	96% (24)	4% (1)	-	25
Sarcops calvus	fruit parts	100% (1)	-	-	1
Total		79% (142)	7% (13)	14% (25)	180

Table 5: Bird species feeding on *Ficus* sp. 3. (Moraceae). 7 – 9 Sep. 1996. Soft red fruits: height 9.0 ± 0.8 mm, range 8.0 – 11.1 mm; width 8.7 ± 0.8 mm, range 7.4 – 10.2 mm; n =20; mean weight of 20 fruits: 0.295 g.

Bird species	Feeding on	Fruits eaten where plucked (n)	Fruits dropped (n)	Fruits handled unseen (n)	n
Coracina striata	fruit, whole	100 % (3)	-	-	3
Hypsipetes philippinus	fruit, whole	66 % (6)	11 % (1)	22 % (2)	9
Loriculus philippensis	fruit, whole	100% (1)	-	-	1
Ptilinopus occipitalis	fruit, whole	100 % (4)	-	-	4
Total		82% (14)	5% (1)	12% (2)	17

Table 6: Bird species feeding on *Ficus* sp. 4. (Moraceae). 6. Sep. 1996. Soft yellow/orange fruits: height 19.7 ± 1.2 mm, range 21.8 – 16.2 mm; width 23.7 ± 1.3 mm, range 20.8 – 26.2 mm; weight 4.6 ± 0.9 g, range 3.0 – 5.6 g; n = 17.

Bird species	Feeding on	Fruits eaten where plucked (n)	Fruits dropped (n)	Fruits handled unseen (n)	n
Dicaeum bicolor	fruit parts	100% (1)	-	-	1
Hypsipetes philippinus	fruit, whole	100% (1)	-	-	1
Total		100% (2)			2

The rates of fruit handling techniques of the same bird species varied across different trees, ranging from two to four. Bulbuls were seen exploiting all four fig species while a flowerpecker, *Dicaeum bicolor,* and a fruit-dove, *Ptilinopus occipitalis* were seen at three of them (Tables 3 to 6). Yet in no case did rates of handling mode differ significantly across trees species (c2 = 1.847, p =0.93; c2 = 4.83, p =0.305; c2 = 4.176, p = 0.124, all other p = 0.386).

However, different bird species behaved differently on one and the same tree. Thus, rates of fruit handling modes on *Ficus chrysolepis* (Table 3) and on *Ficus* sp. 2 (Table 4) differed significantly among birds ($c^2 = 38.677$, $p < 10^{-3}$; $c^2 = 24.716$, p = 0.037).

DISCUSSION

The fieldwork of this study covers the main fruiting season of the West Visayan region (Heideman 1989) and reveals the use of about 29 fruiting tree species by the Philippine Bulbul. Together with additional data from Hamann & Curio (1999) and Heindl & Curio (1999), 49 fruiting trees used by the bulbul for food are now known from this region (Table 2). The range of fruiting trees used by the bird would probably be even larger if a study covered a whole year (see Fukui 1995). Nevertheless, even though only a limited data set is available, one can generalize that free-living bulbuls take nearly all fruits they can handle with respect to size (see also Hamann & Curio 1999). Since bulbuls consume mainly the small fruits (Fig. 2), they can swallow most fruits whole, ingesting all seeds a fruit contains. The maximum width of the large fruits taken by the bird (< 15mm, Table 2, Fig. 2) is in general only slightly larger than its gape size ('beak width' 13.5mm, Table 1). However, some soft fruits of fig trees happen to be larger. Studies show that fruit size correlates with gape size of frugivorous birds (Herrera 1984, Johnson et al. 1985, Snow & Snow 1988). Since bulbuls rarely peck at a fruit they can not swallow whole but eat only bits of it, observations suggest a size limitation for bulbul-fruits at about 20 mm maximum in diameter. In contrast to large-fruited plants used by only a few large and obligate frugivores, the bulbul shares its range of fruit eaten with a lot of other fruit eating birds (Heindl & Curio 1999, Hamann & Curio 1999). Most of these fruit trees belong to early successional forest stages (Hamann

& Curio 1999). This fits the observation that kaingin-placed nets tend to catch more bulbuls than do primary forest nets. Unfortunately, because of the small number of mist nets used in old growth primary forest, this relation can not be quantified.

Only the small fruits of the Tiliaceae (*Microcos stylocarpus*,) were not eaten by any bird. Even after the fruits have dropped to the ground, these remained uneaten. Consequently, it would be interesting to investigate why some fruits within the size range of fruits consumed by the bulbul remain uneaten. Feeding deterrents may involve secondary plant compounds not tolerated by the bulbul/birds (Levey & Cipollini 1998). Yet birds also tend to reject fruits whose seeds are not easy to void, or those which are nutritionally unsatisfactory (Herrera 1981, Sorensen 1984, Johnson et al. 1985, Levey 1987, Stanley & Lill 2002). Today, one can only speculate that the fruit eating specialist able to overcome the feeding deterrent of the fruits of *Microcos* (see Tsahar et al. 2000, Tewksbury 2000) no longer occurs in the area (see Ng 1983).

In general bulbuls feed on the wing, plucking fruits and pecking on the pulp while perched on a branch. Hover-feeding enables bulbuls to reach fruits on slender twigs. As demonstrated by the less agile fruit doves that do not take fruits in flight, such fruits are apparently only available to birds of lesser body weight like the bulbul (Table 1). But this species is only partly frugivorous, as indicated by at least 16% of the examined faeces containing parts of insects. So, like other bulbuls, the Philippine Bulbul is omnivorous but with a clear dominance of fruits in its diet (Rabor 1986, for other *Hypsipetes* spp. see Smythies 1993 and Fukui 1995, for other Pycnonotidae Corlett 1998b, Mlingwa 1998).

If one follows the 'frugivore paradigm' suggested in the seventies (Janzen 1970, Snow 1971, Connell 1971, McKey 1975, Howe & Estabrook 1977, Howe & Smallwood 1982), the bulbul tends to belong to the group of generalist frugivores as described by Howe (1993). The bird is small (Table 1), occurs in large populations, uses many fruiting plant species (Table 2), and complements its fruit diet with a considerable proportion of insects

(Rabor 1986; this study). The bird is a gulper and, hence, does not destroy seeds during ingestion. Seeds are voided apparently intact (Schabacker & Curio 2000). It is likely that the ability of seeds to germinate is not reduced after gut passage. Such data are not available for *Hypsipetes philippinus*, but seeds defecated by *Hypsipetes amaurotis* are still able to germinate after gut passage (Fukui 1995). However, how and to what extent gut passage affects germinability of seeds (see Fukui 1995, Moore 2001) remains to be studied in any single case.

Philippine Bulbuls waste few fruits. They eat the majority of the fruits which they take from the tree. Only a few percent are dropped (Tables 3–6). Even though fruit doves (11% of all caught birds, Fig. 1) also eat the majority of fruits they pluck (Tables 3–6), their value as a seed dispersal agent is limited. First, larger frugivorous birds are much less frequent at forest edges and in the secondary growth forest they also prefer larger fruits (Fig. 1). Second, doves tend to stay in the canopy of the fruiting tree for long periods of time digesting, and hence, void a lot of seeds under the crown (Heindl & Curio 2000). Third, some doves, like *Chalcophaps indica*, are able to destroy seeds in their muscular gizzard (Lambert 1989, Corlett 1998b) and for this reason they are considered seed predators.

A close look at the actual distribution of fruit handling techniques of birds reveals that the fruit-eaters observed behaved rather uniformly regardless of the fig species involved. Bulbuls could be studied most closely because they visited all four figs under scrutiny. There were no among-tree differences in handling. This finding is consonant with the fact that individuals of different bird species exploiting one and the same tree (seven and eight species on two trees) differed significantly from each other in their use of the various handling modes. These species differences evidently translate into species-specific qualities as seed dispersers. Obviously, the handling mode 'eaten' can be fully evaluated only when also looking at visit length in the tree exploited (Heindl & Curio 2000); a species staying long enough for digestion to occur on the spot is necessarily a lower-quality disperser.

Visit lengths of *Hypsipetes philippinus* to fruiting trees are generally shorter (5 to 10 min; Heindl & Curio 2000, pers. observation) than the average gut passage time. The gut passage time of seeds in the Philippine Bulbul varied between 5 and 51 min with a median of 14 min (Schabacker & Curio 2000). Hence, when they do not return to a feeding-tree within minutes, the bird deposits a large fraction of ingested seeds away from the immediate vicinity of the parent tree. Therefore the bird is an effective seed disperser. However, since bulbul flocks tend to stay in the vicinity of a fruiting tree they might disperse the bulk of seeds only over a few meters, therefore, providing within-habitat dispersal. By contrast, gut passage time of up to 50 min may be long enough to result in long distance seed dispersal. Because of its abundance at forest edges, the bird might therefore be a high-quality seed disperser between different habitats.

Birds of some other species disappeared with fruits in their beak into the surrounding vegetation (Table 3-6). Hence, they might disperse seeds with and without gut passage. Both Flowerpeckers observed (*Dicaeum bicolor* and *D. trigonostigma*) carried some fruits in the bill (Table 4). But because they eat only part of the pulp, they may not carry away large numbers of seeds. Also the Coleto (*Sarcops calvus*, Table 3) and a fruit dove (*Phapitreron leucotis*, Table 4) carried fruits in their bill. However, this may not happen too often, with only one observation pertaining to each species. Therefore, bulbuls are responsible for the bulk of fruits/seeds carried off in the beak and dispersed without gut passage from the fig trees examined. Yet the fraction of fruits dispersed by the bulbul without gut passage seems to be small as well (less than 9 – 22%). Although we are not able to estimate the distance the birds fly with the fruit in their beak, it seems most likely that the birds stay in the near vicinity of the observed tree (Heindl & Curio 2000). Hence, the fraction of fruits carried in the bill over long distances and so dispersed without gut passage should be negligible.

Consonant with the escape hypothesis (Janzen 1970, Connell 1971, Howe & Smallwood 1982, Clark & Clark 1984), Philippine Bulbuls provide high-quality seed dispersal. Because of their abundance in primary as well as secondary forest, they are among the most important generalist frugivores/seed dispersers in forest habitats in this region, particularly for small-fruit trees and early successional tree species (Hamann & Curio 1999). Thus they promote the regeneration of clear-felled land.

Acknowledgments

This is contribution No. 45 of the Philippine Endemic Species Conservation Project of the Frankfurt Zoological Society. The study was carried out under the aegis of a Memorandum of Agreement between the Department of Environment and Natural Resources, Philippines and Ruhr-University Bochum, Germany. The project received financial support from: Bird Breeders Association (AZ), Daimler Chrysler Foundation, European Union, Frankfurt Zoological Society, German Ornithologists' Society (DO-G), Andreas Stihl Foundation, Pentax, Swiss Society for Bird Protection (SVS), as well as from H. Langer, E. Mayr, C. Sudhoff, E. Thomas, and P. Wüst. The assistance of the Protected Area and Wildlife Bureau (Director W. Pollisco) of the DENR of Region VI, and the Negros Forest and Ecological Foundation, Inc. (Gerry Ledesma) is gratefully acknowledged. We especially appreciate the untiring help in the field of E. Panganiban (Negros) and B. Tacud (Panay), and of T. Kalenschere with computation.

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