

FRUIT CHARACTERISTICS AS DETERMINANTS OF GUT PASSAGE IN A BULBUL (*HYPSSIPETES PHILIPPINUS*)*

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Abstract. Plants benefit from animal-mediated seed dispersal when their seeds are taken to places suitable for growth. Plants may have evolved mechanisms to optimize the area covered (seed shadow), seed density, and distance of seeds from the parent, in order to escape mortality by seed predators *s. l.* and/or maximize the number of safe sites for germination. With endozoochorous seed dispersal, plant species might increase gut passage time (GPT) to extend dispersal distance. We first suggest the hypothesis that those fruit characteristics influencing dispersal distance fit requirements for seedling establishment. In this study we compared the GPT of different fruits eaten by the Philippine Bulbul (*Hypsipetes philippinus*) to look for relationships with fruit characteristics and seed ecology. We found that the species of fruit influences GPT of seeds. GPT was found to increase with nutrient (sugar, protein) content, whereas it is decreased by both a large seed and a high seed load. Relationships between GPT and seed ecology are discussed. Pioneer trees, which are known to depend on wide dispersal of their seeds, are thought to slow GPT through a higher proportion of nutrients extending retention time of pulp, and a lower proportion of indigestible seeds. Conversely, seeds of plants that thrive on spatially restricted resources, and thus depend on short-range dispersal, have shorter GPTs and fruits with the opposite features. Accepted 27 December 2000.

Key words: Bird-mediated seed dispersal, gut passage time, pioneer tree, fruit, nutrient, *Hypsipetes philippinus*.

INTRODUCTION

Birds use fruits as a source of nutrition, especially in the tropics. Seeds ingested with fruit pulp are regurgitated or defecated in viable condition (Sorensen 1984; Johnson *et al.* 1985; Levey 1986, 1987). Excepting cases of seed predation (Dirzo & Domínguez 1986, Snow & Snow 1988, Green 1993, Corlett 1998), birds are thus important seed dispersers in wooded habitats (van der Pijl 1972, Stiles 1980, Howe & Smallwood 1982).

Plants gain advantages from endozoochorous seed dispersal because their seeds are scattered over a certain area, the "seed shadow." The study of seed dispersal mechanisms has revealed several benefits to the plant. Spacing of siblings reduces intraspecific competition between neighbors (Janzen 1970, Dirzo & Domínguez 1986, Stiles & White 1986). As a result of seed dispersal, seedlings escape higher mortality near the parent ("escape hypothesis"; Janzen 1970,

Connell 1971, Howe & Smallwood 1982, Clark & Clark 1984). Dispersal of seeds also increases the likelihood of finding a site suitable for germination and successful reproduction ("safe site" or "colonisation hypothesis"; Platt 1976, Howe & Smallwood 1982, Herrera 1985, Dirzo & Domínguez 1986). The likelihood of seeds reaching a safe site increases with dispersal distance (Green 1983, Geritz *et al.* 1984). On the other hand, dispersal can also carry disadvantages. For example, when seeds leave the microhabitat to which they are adapted they are unlikely to establish. Thus, some plants show adaptations to reduce long-distance dispersal of their seeds (van der Pijl 1972, Strasburger *et al.* 1991).

In all cases mentioned above, the dispersal distance is of some importance. Typically, the density of seeds is highest near the parent and declines leptokurtically, with humps possibly superimposed (Wenny & Levey 1998) with increasing distance (Levin & Kerster 1969, Schaal 1980). Studies show that the mean dispersal distance from the parent depends on the bird's behavior after ingesting the fruit and on how long the seeds remain in the gut (Murray 1988, Murray *et al.* 1994, Sun *et al.* 1997). We hypothesize

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that some plants have evolved mechanisms influencing the dispersal distance of seeds, i.e., optimizing area covered, seed density, and distance of seeds from the parent, thus maximizing the number of safe sites with successful germination.

Recent studies have supported the idea that plants can influence what happens to their seeds after ingestion (Murray *et al.* 1994, Wahaj *et al.* 1998). In particular, a plant might manipulate the gut passage time (GPT) of seeds and hence the dispersal distance. It has been known for a long time that the composition of food has an influence on avian gut function and thus on evacuation time (Sturkie 1976). Features of a fruit, such as seed size (Levey 1986, Levey & Grajal 1991, Sun *et al.* 1997) and proportion of dry matter of fruit pulp (Levey 1986), influence seed passage. Until recently the nutritive value of fruit pulp was mainly examined with regard to the nutritional requirements of various bird species (Snow 1971; Stiles 1980; Howe & Vande Kerckhove 1980; Sorensen 1981, 1983, 1984; Johnson *et al.* 1985; Howe & Westley 1988; Levey & Grajal 1991). This study focuses on the influence of fruit characteristics on seed passage time in a Philippine bulbul in order to look for relationships to seed ecology. The bird species studied is the most abundant frugivore in the study area in NW Panay, Philippines (pers. obs.). The following questions are addressed: Do seeds of different tree species have different passage rates? To what extent is the passage time of seeds determined by fruit characteristics? Which fruit characteristics influence the gut passage of the seeds, and do these characteristics delay or shorten GPTs?

MATERIAL AND METHODS

The study was conducted in and around the research station of the Philippine Endemic Species Conservation Project (PESCP) in the Philippine archipelago in the NW of the island of Panay (11°49.2' N, 121°58.1' E). The station is at 450 m a.s.l. and is surrounded by the mosaic of primary and secondary forest of an upland rainforest. During summer and winter (June 1997 to January 1998) 80 feeding trials were carried out with briefly captive Philippine Bulbuls (*Hypsipetes philippinus*) and indigenous fruits. By virtue of its relative abundance (c. 50 % of all net captures, pers. obs.), the Philippine Bulbul is one of the major frugivorous birds in primary and secondary forests in this area. It is mainly an omnivorous bird but with a clear dominance of fruits in its diet (Rabor

1986; for other *Hypsipetes* species, see Fukui 1995). Fruits for feeding trials were collected from the seasonally available range of fruit of the bulbul as based on preliminary observations of fruiting trees/shrubs and examination of feces. In some cases, direct observation failed to ascertain the use of a fruit species by the bulbul, but the birds readily took these fruits in the cage even though fruits known to be eaten by them in the wild were present as well. We feel confident that those fruits are also part of its food in the wild. Fruits for the feeding trials and chemical analyses were collected in all but two cases from a single individual tree to maximize uniformity among fruits; in the case of two understory fruit species (*Psychotria* sp. and *Lasianthus morus*) a single shrub did not provide enough fruits so they were taken from a few individuals. Fruits of the same sample of trees were collected in the same ratio for both the feeding trials and chemical analysis.

Passage-time measurements

Birds were mistnetted and, when fulfilling the criteria for maintenance (as per Memorandum of Agreement with the Department of Environment and Natural Resources), put as soon as possible in an outdoor cage (dimensions 0.7 × 0.9 × 0.9 m) which was prepared with fresh fruits of one species. The inside of the roof and sides of the cage were lined with soft fishing net to prevent injury to the bird. Availability of birds and of sufficient amounts of fresh fruits at the same time determined the number of replicates of the feeding trials with a certain fruit species. The birds were weighed before starting the feeding trial to monitor potential weight changes before releasing the birds. Depending on the frequency with which nets were monitored, the experiment started within 90 min after the bird had been netted. Since birds were released immediately after a feeding experiment they were not given any kind of artificial food. Birds were observed from behind a screen during the experiment that lasted 60 min. They remained undisturbed throughout the trials and seemed unaware of the observer's presence. They soon relaxed and showed natural behavior like singing, preening and bathing in a water bowl. Fruits and water were available *ad libitum* all the time. Due to transportation (distance from net to cage) after capture, an average of 38 ± 23 min (n = 33) passed before starting the trial. While in the net or bag, the birds usually defecated. Because of the short retention times known for frugivorous birds (Sorensen 1984, Worthington 1989, Karasov & Levey

1990), the type of fruit eaten before capture and hence voided thereafter, but prior to a feeding trial, was known in most cases. The seeds of the experimental fruit and the fruits previously eaten could thus be distinguished in the feces. If the bird had not defecated in the bag we analyzed only those trials in which seeds not used in the experiment appeared. In other words, we ruled out situations in which a bird had seeds of the test fruit in its gut previously, which could cause a bias towards a shorter gut passage time. Time and location of every defecation were recorded during a trial. It is important to report seed passage time because birds treat seeds and fruit pulp differently in the gut (Levey & Grajal 1991, Levey & Duke 1992). For statistical analysis, the time between the first fruit eaten by the bird and the first defecation containing seeds of this fruit type (GPT, equivalent to "transit time" *sensu* Levey & Karasov 1994) was recorded. This was the measurement with the greatest accuracy for fruits varying in the number of seeds per fruit. Thus the GPT in this study is different from the mean retention time (i.e. mean of passage time of 50% of ingested seeds) (Karasov & Levey 1990) which diminishes variance in the data. Because the birds were not adapted to human presence it was important to prevent even slight disturbance during a trial. So it was not possible to make any further manipulations (like changing the paper on the cage floor) to get another measure of GPT after the observation had started. However, any influence of fruit characteristics on the gut passage of the first seed can be expected to be the same for the following seeds of a meal of the same fruit species.

If a bird had not taken the first fruit within one hour we abandoned the experiment in favor of another bird. With a few exceptions, birds ate the first fruit within 15 min (6 ± 6 min, $n = 35$). After the experiment, the birds were weighed again and released. They all appeared to be healthy and unharmed with no or only slight weight loss ($< 2\%$). It is possible that the experimental situation had influenced the GPT measured due to stress or the short fasting period. However, since all birds had undergone the same treatment prior to the experiment, experimental birds were thought to be comparable in their state of stress, etc.

Fruit characteristics

To examine fruits in detail, we collected additional fresh fruits for measuring physical characteristics and for drying. Length (apex to base) and width (greatest

diameter) of fruits and seeds were measured with calipers. Their volume was estimated using a measuring cylinder. Fruits and seeds were weighed fresh. Unless otherwise noted, the mean \pm standard deviation of 20 fruits/seeds per species is given. The average seed number from fruits with more than two seeds was computed by examining about 50 fruits. For drying, a homemade oven was used. After drying, the water content of pulp could be calculated. The dried fruit pulp was stored for chemical analyses in paper bags in Nalgene bottles with roasted rice. Indicator silicagel was used to check for moisture and the rice was changed whenever necessary.

For nutrient analysis, about 2 g of dried fruit pulp was ground in a plant mill and passed through a 2 mm sieve. Samples were analyzed quantitatively for their proportions of soluble sugar (as equivalent of sucrose after acid hydrolyzation of 50 % methanol extract, Kates 1972), simple sugars (glucose and fructose, with an enzyme analyses kit from Boehringer-Mannheim following water extraction for 2 h), and extractable protein (with BioRad protein assay as equivalent of bovine serum albumin: Bradford 1976; extraction with 0.1 NaOH: Eze & Dumbroff 1981). Total lipid content of fruit pulp was measured using 1 g of ground pulp in a petroleum-ether extraction for 4 days at room temperature and weighing the remaining material (Wrangham et al. 1993).

Statistical analyses

For statistical analysis the software programs EXCEL 5.0 and SPSS 6.13 were used. In all tests, alpha was 0.05 and we give medians and/or means \pm SD, where appropriate.

Because all birds were used only once in feeding trials, controlled for by bird rings, GPT values are statistically independent. For parametric tests we used log-transformed values, giving a normal distribution (Shapiro-Wilks $P = 0.46$).

Retention times of seeds of different tree species were compared using an ANOVA. We used fruit characteristics as "within" variable and retention time as the dependent variable.

The influence of fruit characteristics on GPT was estimated first with a multiple regression model, in which all independent variables were entered at the same time. The estimation of the regression coefficients becomes unstable with increasing collinearity among the variables, therefore the variables used in a regression analysis should be independent. Accordingly, we used only fruit characteristics that did

not show high correlations between each other (i.e., $r < 0.70$, $P > 0.05$). For this reason the values of total sugar and simple sugars, as well as values of dried fruit pulp and all nutrients, could only be used in a bivariate correlation. Additionally, those independent variables not attaining significance in the multiple regression model were tested for a potential effect on GTP by bivariate correlation analysis.

To compare all fruit characteristics, we correlated both the water and nutrient contents as well as the seed load (g and vol.) with the whole fruit (wet mass or volume as 100 %). Because it was impossible to measure the nutrient composition of individual fruits, we used the mean value of a large number (from 2 g of dried fruit pulp) of fruits in the analyses. This procedure missed the existing variance among the fruits of one tree. However, we deemed the error small because the within-plant coefficient of variability ($cv = [\text{standard deviation} / \text{mean}] \times 100\%$) of a fruit species is small for known individual fruit characteristics (mean $cv \pm SD$ for individual characters over n fruit species: fruit height $8.6\% \pm 3.6\%$; fruit width $7.1\% \pm 3.6\%$; seed height $6.1\% \pm 2.9\%$; seed width $8.3\% \pm 3.4\%$, $n = 15$) compared with that of GPT ($38.9\% \pm 15.1\%$, $n = 7$). Birds also usually swal-

lowed more than one fruit, with the exception of large fruits. So, comparable to the procedure for the chemical analysis, they took a sample of several fruits in one bout.

RESULTS

Fruit characteristics

Fieldwork revealed the consumption of fruits of 21 tree species by bulbuls. Bulbuls were not seen feeding on trees with very large fruits (much larger than gape size: 13.5 ± 1.9 mm, $n = 107$) and they do not peck at fruits to eat the pulp only. The height of the fruits ranges from 19.2 ± 1.0 mm to 3.9 ± 0.6 mm, the width from 14.0 ± 0.8 mm to 4.2 ± 0.2 mm. But the bird is not an exclusive frugivore; 16 % of 57 examined fecal samples contained parts of insects.

The nutrient values of 13 fruit species could be analyzed (Fig. 1). Based on dry weight, the measured features of fruits relevant to digestion are a high water content ($83 \pm 11.2\%$, $n = 13$), indigestible seed load ($26.2 \pm 15.4\%$, $n = 13$), and the low concentration of nutrients: protein content ($2.5 \pm 1.1\%$, $n = 13$), lipid content ($6.9 \pm 10.8\%$, $n = 12$), and content of soluble sugars ($5.8 \pm 2.9\%$, $n = 13$) (Fig 1).

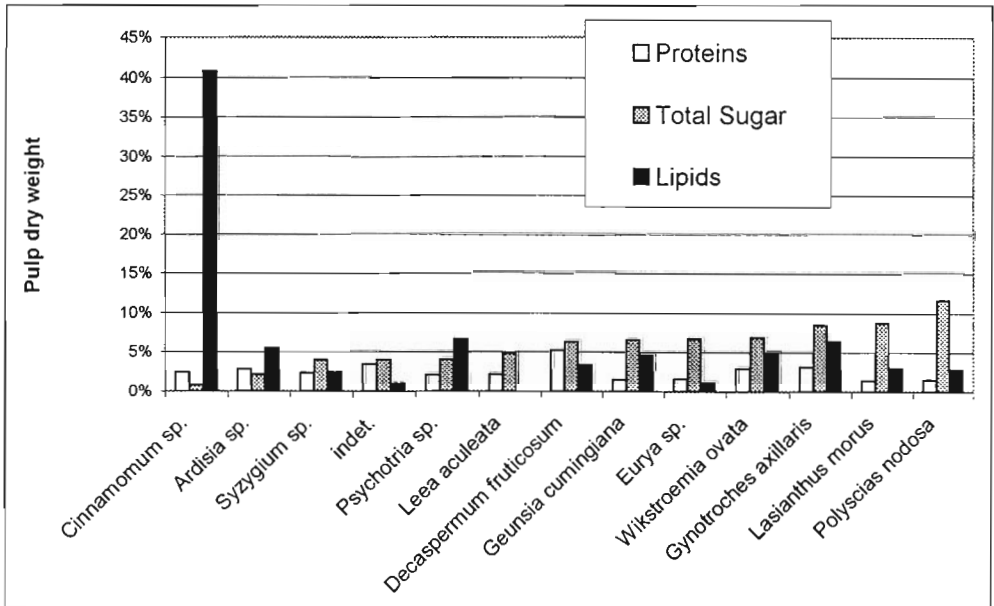


FIG. 1. Protein, lipid and sugar content of the examined fruits (as measured by percentage of pulp dry mass). There are no lipid values for *Leea aculeata*. Indet. = unidentified fruit.

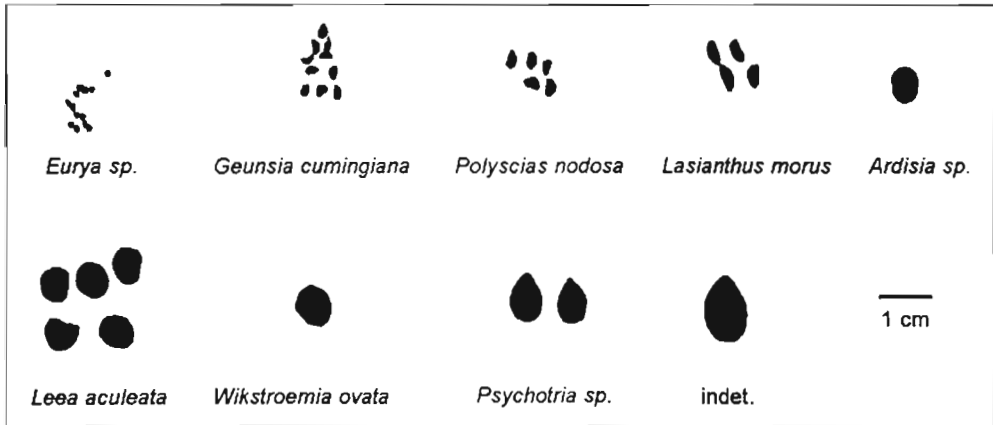


FIG. 2. Illustration of the number and dimensions of seeds of one fruit of each species. See also caption to Fig. 1.

The characteristics of fruits eaten by bulbuls are highly diverse among different species. The water content in the pulp ranges from 50 % (*Cinnamomum*) to 95 % (indet., an unidentified Meliaceae). The proportion of wet fruit mass made up of pulp ranges from 42.1 % in *Cinnamomum* sp. to 93 % in *Lasianthus morus* (73.8 ± 15.4 %, $n = 13$). Therefore seed load of fruits varied between 7 % and 57.9 %. The seed sizes (Fig. 2) differed among fruits by a factor of 14 and decreased with the number of seeds a fruit contains ($r = -0.74$, $P = 0.005$, $n = 12$; $r = -0.75$, $P = 0.005$, $n = 12$; length and width of seeds respectively).

Seed load decreased with increasing seed number ($r = -0.58$, $P = 0.046$, $n = 12$). Therefore fruits with one large seed contained relatively less pulp and probably, as a result, relatively less nutrients. Among the fruits examined the content of sugar increased with increasing seed number ($r = 0.64$, $P = 0.025$, $n = 12$). Therefore there is a trend for fruits with plenty of small seeds to offer more sugar. The correlation of seed number and lipid or protein is non-significant.

Protein content ranged from 1.4 % in *Lasianthus morus* to 5.3 % in *Decaspermum fruticosum*. Fruits of *Cinnamomum* sp. are remarkably rich in lipids (40.8 %) compared with 3.8 ± 2.0 % ($n = 11$) of all other fruits together (Fig. 1). The content of soluble sugars (Fig. 1) differed among fruits by a factor of about 15, ranging from 0.79 % (*Cinnamomum* sp.) to 11.66 % (*Polyscias nodosa*). Glucose and fructose values differed by a factor of 6 or 7. Both these sugars varied in their contribution to the total sugar content

of different species (30% in *Syzygium* to 63% in *Leea aculeata*). The total sugar content correlated positively with the content of both fructose ($r = 0.85$, $P = 0.007$, $n = 8$) and glucose ($r = 0.86$, $P = 0.005$, $n = 8$), but it is larger than that of fructose and glucose together.

Passage-time trials

Nine fruit species that had been subjected to a complete nutritional analysis and at least two (generally 5–7) feeding trials were used in the statistical analysis of the passage-time trials (Fig. 3). In these species, bulbuls ingested the fruits whole and did not discard seeds before swallowing. They also defecated nearly all seeds. Only two seeds were regurgitated. Because seeds of the same species, as well as even larger seeds than those that were regurgitated, were defecated, we think these cases were exceptions and we did not include these trials in the analyses. After gut passage, seeds showed no visible damage. Large seeds (Fig. 2 second line) were defecated together with only small amounts of digested pulp; small seeds (Fig. 2 first line) were defecated within a large amount of pulp.

The measured GPT varied between 5 and 51 min (17.0 ± 10.5 min [mean \pm SD], $n = 47$; median = 14 min, $Q_{25\%} = 11$ min, $Q_{75\%} = 21$ min). The standard deviation of GPT is greater for fruit species with a long GPT. The species of fruit significantly influences the GPT of seeds (see Fig. 3). Those three species with longest GPTs (*Geunsia cumingiana*, indet., *Polyscias nodosa*) show significant differences compared with species with the shortest GPTs (*Psychotria* sp.,

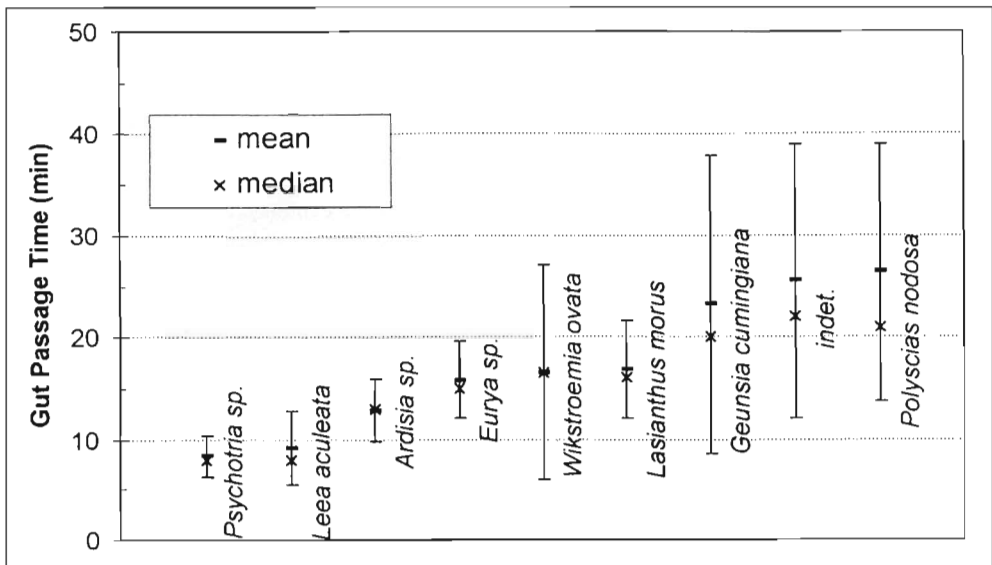


FIG. 3. Median (to mirror skew), mean and standard error of GPT; 5–7 feeding trials per tree species (2 for *Wikstroemia ovata*). Fruit type significantly influences the GTP of seeds (ANOVA $F_{8,38} = 5.68$, $P = 0.0001$, $n = 47$). The two tree species with shortest GPT differ significantly from the three with longest GPT (after Bonferroni correction). See also caption to Fig. 1.

Leea aculeata) (after Bonferroni correction). The variation in GPT explained by fruit characteristics is D (coefficient of determination) = 0.54.

We examined different characteristics of fruits together for their effect on seed passage in a multiple regression model (Table 1). The characteristics of fruits entered into the model and relevant to digestion were concentration of nutrients, water content, size (= length) of the indigestible seeds and seed load as measured by percent of volume. Both an increasing sugar content and a large seed increase GPT (see Table 1, for seeds see below). Conversely, both a high water content and a high seed load decrease GPT (see Table 1). The effects of lipid or protein content on GPT do not attain statistical significance.

In bivariate correlation, GPT increases with increasing proportion of dried pulp a fruit supplies ($r = 0.51$, $P < 0.001$, $n = 47$), simple sugars ($r = 0.50$, $P = 0.001$, $n = 42$; $r = 0.42$, $P = 0.005$, $n = 42$; fructose and glucose respectively), and protein ($r = 0.57$, $P < 0.001$, $n = 47$). This latter result is at variance with that of the multiple regression analysis (see above). A reasonable explanation might be that proteins interact with other nutrients so that their GPT prolonging effect is more apparent than real. Con-

sumption rate (weight of fruit eaten in 15 min) is not correlated with GPT ($r = -0.21$, $P = 0.17$, $n = 47$), though such a relationship is well established by other studies (e.g. Levey & Martínez del Río 1999).

TABLE 1. Sign and strength of the influence on gut passage time of different fruit characteristics with their significance as tested in a multiple regression. Gut passage increases with increasing sugar content and seed size (= length) (but see Fig. 4). Conversely, gut passage decreases with increasing water content and large seed load. Lipid or protein content do not seem to affect gut passage.

Characteristic	Sign and Strength*	Significance
Sugars	0.841	$P = 0.005$
Proteins	-0.707	$P = 0.141$
Lipids	-0.247	$P = 0.140$
Water content	-1.808	$P = 0.018$
Seed length	0.788	$P = 0.016$
Seed load (vol %)	-1.353	$P = 0.030$

* Standardized coefficient of multiple regression (β)

The effects of most of the fruit variables are monotonous. However, the influence of seed size on the GPT differs from this pattern as shown in Fig. 4. There is a decrease of GPT with increasing seed height in the range from 1 to 8 mm which is significant in a bivariate correlation (see Fig. 4), whereas the 12 mm long seeds of *indet.* (= unidentified) have an unexpectedly long GPT.

DISCUSSION

Passage-time trials

Being a non-destructive gulper of fruits, and visiting fruit trees for usually less than 10 min (Heindl & Curio 1999, pers. obs.), the Philippine Bulbul must be an important seed disperser. Passage times of seeds through the digestive tract of temperate and tropical birds are generally short (Herrera 1984, Sorensen 1984, Johnson *et al.* 1985, Levey 1986, Worthington 1989, Whitney *et al.* 1998). Our data on GPT

of seeds in *Hypsipetes philippinus* do not differ from the expected range of values for a bird of this size, as derived from comparable studies also using wild fruits and giving data of first appearance of seeds (Walsberg 1975, Sorensen 1984, Worthington 1989, Sun *et al.* 1997).

Seeds of different tree species vary markedly in their passage time through the bulbul's gut (Fig. 3), thus confirming the results of Sorensen (1984) and Sun *et al.* (1997) for other species. At least 54 % of the variation in GPT is explained by fruit characteristics. Therefore GPT of a seed must be influenced by features of the fruit, i.e., seed and/or fruit pulp. A large part of the remaining variation may be due to individual needs and circumstances (state of nutrition, state of stress; Surkie 1976, Clench & Mathias 1992, Duke *et al.* 1980). Because of the linear model used in this study, it is likely that the influence of fruit characteristics on gut passage is underestimated. In mammals, a linear influence of the water content of

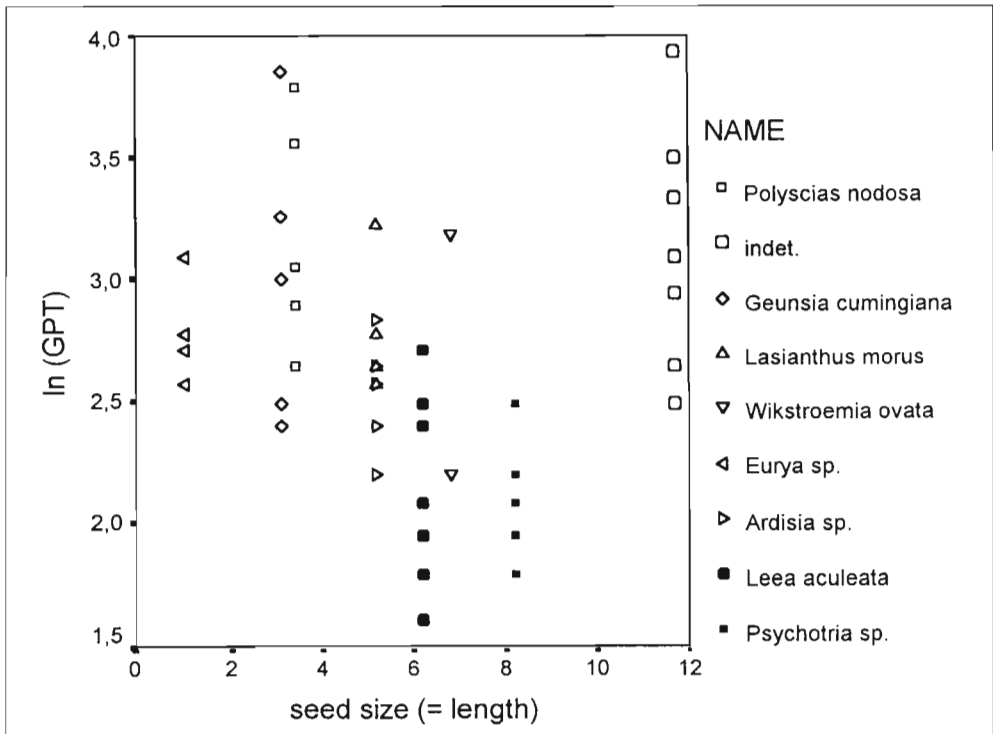


FIG. 4. GPT decreases with increasing seed size within a range of 1 to 8 mm. The GPT correlates significantly with seed size ($r = -0.55$; $P < 0.001$, $n = 40$) if *indet.* (= unidentified fruit) is not considered.

seeds was found by Reid & Brooks (1994). However, with complex food (mixture of seeds and insects) the influence of food components on gut passage is non-linear (Reid & Brooks 1994). The present results support the hypothesis that plants might control the GPT of their seeds and thereby influence the pattern of their dispersal (Murray *et al.* 1994, Wahaj *et al.* 1998, Karasov 1999).

The study by Murray *et al.* (1994) of plant secondary metabolites and their influence on GPT is under debate (Witmer 1996, Wahaj *et al.* 1998). It remains unknown which compound is responsible for the laxative shortening effect proposed by Murray *et al.* (1994). We suggest another mechanism by which a plant can influence GPT in endozoochorous fruits. Plants could gear their pulp nutrient composition and their seed characteristics, e.g., size and load, to optimizing seed shadow. Though our results are compatible with the GPT manipulating hypothesis, they are not experimental.

Pulp nutrient concentrations and seed characteristics vary markedly among different fruit species (Fig. 1, Fig. 2). The multiple regression model identified the contributions of various fruit features to GPT. Some of the nutritional components of (dried) fruit pulp, particularly sugar, extend the GPT of the accompanying seeds (Table 1). Also a higher protein level increases GPT, as assessed by bivariate correlation. Conversely, a large proportion of indigestible bulk such as a high seed load (Table 1) and large (but not overlarge) seeds (Fig. 4), as well as high water content, speed up gut passage (Table 1). The influence of water content may be indirect, caused by a dilution of nutrient concentration of pulp during passage in the small intestine. Water absorption takes place mainly in the lower part of the intestinal tract (Denbow 2000).

Therefore our results parallel those of Witmer (1996, 1998a, 1998b), Karasov (1999), and Levey & Martínez del Río (1999), who found slower passage rates in fruit diets with higher sugar concentration in passerine species. Rates of processing of digesta are closely tied to rates of absorption (Afik & Karasov 1995, Witmer 1998a, Karasov 1999). This is a common phenomenon in birds and mammals, where retention time is related to luminal solute concentration, mediated by a negative feedback due to neuronal and hormonal mechanisms (Duke 1989). An optimality digestion model that assumes maximization of net rate of energy gain will predict shorter retention times for animals eating energy-rich food

(Sorensen 1984, Martínez del Río & Karasov 1990, Levey & Karasov 1994, Karasov 1999). This model was invalidated by results obtained with Cedar Waxwings by Levey & Martínez del Río (1999), in line with our findings. These fit best to the "osmotic constraint" model of Levey & Martínez del Río (1999). Similarly, lipid and protein, when added to a bird's diet, can increase passage time (Denbow 2000). In the present study there is no significant influence of lipids on GPT. However lipids are also known to slow intestinal motility (Roby *et al.* 1989).

The reasons for differences in the findings are not clear. The analysis of fats with non-polar solvent yields a complex mixture of lipids (e.g., fatty acids, glyco-, phospholipids, waxes, ethereal oils, lipo-soluble vitamins, phytopigments). Each of the substances has its own nutritional quality and a few may even be toxic to some species (Herbst 1995). The missing influence of lipids on GPT in this study may be due to the unspecificity of lipid analysis. The processes by which vertebrates assimilate different lipids are rather specific and there are no consistent patterns in the assimilation of fats (Carey *et al.* 1983, Bairlein 1999). Therefore different bird species may react in varying ways to food features due to different specialization to fruit diets (Martínez del Río *et al.* 1988, Levey & Karasov 1994, Witmer & van Soest 1998) or with changing nutrient requirements. Digestion data in publications are often difficult to compare because of unequal captivity conditions. Experiments are often conducted with captive birds acclimatized to artificial diets in the long term. This influences gut morphology (Levey & Duke 1992) and changes in digestion may occur as well (Witmer 1998a). In our study, the bird's natural diet was withheld for no more than 2 to 3 hours and their response in terms of retention time was presumably more natural.

Even though larger particles are generally retained longer in a bird's digestive tract (Denbow 2000), it has been shown by Levey (1986) and Levey & Grajal (1991), and corroborated by this study, that frugivorous birds defecate large seeds faster than small seeds. But beyond a certain seed size it probably becomes more difficult to pass an overlarge seed through the gut (Fig. 4). A large number of frugivorous birds are able to regurgitate particularly large seeds (Sorensen 1984, Levey 1986, Levey 1987). Regurgitation is usually the faster way to void seeds and enables birds to increase their rate of nutrient intake (Sorensen 1984, Levey 1986). However, although bulbuls are

able to regurgitate seeds they still often defecate the largest ones. Why? Results (Levey 1987, Worthington 1989) show that the technique of seed regurgitation often hinders swallowing a new fruit. Hence regurgitation of seeds is not always the best solution to optimize net energy gain. A recent study provides evidence that seeds in the digestive tract do not hinder the uptake of sugars (Witmer 1998a). Direct observation of bulbuls showed that they were able to swallow several of the large fruits of indet. (= unidentified) in one bout.

Fruit characteristics and seed ecology

The link between GPT, animal movement patterns, and dispersal distance is not yet clear but in general a long GPT of seeds increases the dispersal distance (Murray 1988, Clench & Mathias 1992, Murray *et al.* 1994, Sun *et al.* 1997). Many things, such as frequency of defecation, number of seeds/defecation etc. will affect that link. Because of the large variation in GPT for fruits with longer GPTs (Fig. 3) the dispersal of these seeds would also cover a larger area.

Because reciprocal selection pressures have not resulted in tight coevolutionary relationships between fruiting plants and frugivores, any coevolution appears to involve guilds and leads most likely to diffuse fruit dispersal mutualism (Howe & Westley 1988). For this reason we suppose that a mechanism effective in many bird species of different genera is likely to occur. An effect due to nutrient concentration would work with all birds that have adopted the same digestion strategies. This would also be a robust mechanism since birds would not evolve counteradaptations as they would against laxative chemicals (see Murray *et al.* 1994, Wahaj *et al.* 1998), which are probably costly because they decrease digestive efficiency.

From the results of this study and published literature we can devise features of fruits that should affect GPT. Fruits requiring more time to extract nutritional parts of the pulp, i.e., fruits with a high percentage of sugars and/or protein, and/or lipids, little water and a low proportion of indigestible seeds tend to have a longer GPT. Because the seed load decreases with increasing seed number there is a trend for a longer GPT of fruits with many small seeds. Is the type of fruit syndrome connected with a certain reproductive strategy of a tree species? The data of this study tend to support this idea.

There are two known strategies for regeneration of trees that are distinguished by germination and

seedling establishment: climax and pioneer tree species (Whitmore 1993). The two strategies are known to involve seeds of different sizes and to use different strategies for seedling survival, associated with two different types of habitat patchiness. One is the patchy occurrence of tree-fall gaps, the other special requirements of the parent. Following Whitmore (1993), pioneer species have lots of small seeds which are easy to disperse. They require at least partly full sun for germination and grow only in large gaps (Whitmore 1993). Large gaps are scarcer than small ones (Brokaw 1982) and so plants gain from a long dispersal distance (Geritz *et al.* 1984). The importance of long-distance dispersal agents becomes obvious in forestry during recolonization of clear-cuttings (Strasburger *et al.* 1991). Canopy trees of the secondary forest in the study area, and therefore expected (*Geunsia cumingiana* and *Gynotroches axillaris*) or known (*Decaspermum fruticosum* and *Polyscias nodosa*; Merrill 1967) to be pioneer trees, have sugar-rich fruits (6–12 %, Fig. 1) with a lower water content in the pulp (80–83 %), small seeds (1–3 mm, Fig. 2), and a low seed load (10–20 %). Accordingly they would be adept at inducing long passage times for seeds (see Fig. 3), and hence long dispersal distances as postulated.

Long-range dispersal is not necessarily beneficial. Plants living in patchy environments, or species very specific in their habitat requirements, might crucially depend on a shorter dispersal distance preventing most seeds from being dropped on unsuitable ground. If safe sites are restricted to a small area around the parent, plants benefit from a smaller dispersal distance (Geritz *et al.* 1984, Grace 1991, Lechowicz & Bell 1991). This could be true for trees of restricted habitats, for example for plants adapted to the moist area near rivers. *Leea aculeata* could be one of those trees. It is characteristically found near rivers and rain drains (Merrill 1967). This tree has fruits with a higher water (91 %) and a lower sugar content (4.8 %, Fig. 1), and a larger seed load (35 %, Fig. 2). The seeds are voided by the bird after a significantly shorter time than those of other species (Fig. 3). This can be understood as an adaptation to a shorter dispersal distance. This may also be the strategy of the seeds of *Psychotria* sp., which is found patchily distributed in the understorey of both secondary and climax forest. Large seeds are also voided more quickly by birds than small seeds because they are more likely to be regurgitated (Levey 1987). We know that plants that depend on spatially restricted resources often have large seeds (e.g., tree species of primary forest; Whitmore 1993).

This study leads us to look for fruit characteristics correlated with seed ecology. Whether these fruit characteristics have been *designed* to manipulate the seed-disperser remains to be shown by further studies.

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