

## FRUIT SIZE, GAPE WIDTH, AND THE DIETS OF FRUIT-EATING BIRDS<sup>1</sup>

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**Abstract.** In most animals, especially those that must swallow food items whole, prey size is related directly to predator size. This paper examines gape limitation and the influence of fruit size on diet in fruit-eating birds, drawing on data gathered over a 5-yr period on 70 bird species and 171 plant species in the lower montane forests of Monteverde, Costa Rica. The results suggest that fruit-eating birds face many of the constraints imposed on other gape-limited foragers, but have an unusual minimum-size relationship with their food because of the unique characteristics of fruits. Fruit-eating birds with broad gapes consumed more lauraceous fruit species and a larger mean and maximum size of fruits overall than narrow-gaped birds. However, the size of the smallest fruits eaten was not correlated with gape width; large-gaped species commonly fed on diminutive fruits. Birds effectively selected among individual fruits within a tree on the basis of fruit size, dropping bulky fruits beneath the tree. Effective size selectivity also occurred among trees of different species in the same family and among plant species in various families. The diet of broad-gaped birds was not comprised differentially of large fruit species. For example, Three-wattled Bellbirds favored medium-sized fruits, whereas Long-tailed Manakins took individual fruits in the same proportions as they took fruit species of different mean fruit diameters. Gape limitations and effective size selectivity have obvious consequences for seed dispersal patterns: plants with large fruits attracted fewer species of birds than plants with small fruits. Moreover, the broad-gaped bird species on which large-fruited plants specialized were those with the most generalized diets.

**Key words:** body size; Costa Rica; frugivory; fruit-eating birds; fruit size; gape-limited predators; gape width; seed dispersal; size selectivity; tropical forests.

### INTRODUCTION

Most fruit-eating birds feed on only a portion of the diversity of fleshy fruits produced in any habitat (Snow 1970, Snow 1981). Fruit selection presumably depends on the behavior, morphology, and nutritional requirements of birds, the abundance of alternative food resources, and fruit characteristics such as temporal availability, habitat, taste, color, abundance, and placement on a plant (Thompson and Willson 1978, 1979, Denslow and Moermond 1982, Howe 1982, Morden-Moore and Willson 1982, Sorensen 1983, Wheelwright and Janson 1985). Fruit characteristics such as pulp-to-seed ratio and nutrient composition also partly determine the net value of a fruit (Howe and Vande Kerckhove 1980).

Fruit size may be critical to selection, but it has been given surprisingly little consideration, despite the demonstration in many foraging studies that the sizes of predators and prey are often positively correlated (Hespenheide 1973, Wilson 1975). Small-fruited plant species have been hypothesized to attract more species of birds than large-fruited ones (Terborgh and Diamond 1970), although Kantak (1979) found that intermediate-sized fruits drew the largest number of bird species among the five plant species she studied in Mexico. Bill size in Panamanian flycatchers and tanagers appeared to be correlated with the size of pre-

ferred fruits (Leck 1971). Diamond (1973) reported that New Guinea fruit pigeons ignored fruits that were small relative to their own size; big birds ate big fruits, medium birds ate medium fruits, and so on. Snow (1973) noted the correspondence between bellbird (*Procnias* spp.) gape widths and the sizes of their favored fruits, species in the Lauraceae, and recognized that fruits, if too large, would not attract seed dispersers.

This paper explores the patterns, mechanisms, and consequences of effective fruit size selectivity by birds in a species-rich tropical forest. In particular, it examines whether gape size constrains a bird's diet and whether large fruit size restricts the number of bird species that can serve as potential seed dispersers for a plant species. Most fruit-eating birds are "gape-limited" (Zaret 1980). They typically swallow fruits whole, although a few soft fruits such as *Ficus* spp. may be eaten piecemeal. Even tanagers, which commonly mandibulate fruits to remove seeds, cannot handle large fruits (D. Levey, *personal communication*; N. Wheelwright, *personal observation*).

The following predictions were tested. As in many gape-limited predators (Zaret 1980), (1) size of the largest fruit eaten by birds should be closely correlated with gape width, (2) large birds should eat more fruit species and a wider range of fruit sizes, and (3) mean size of fruits included in the diet should be positively correlated with gape width. However, in contrast to the case of many carnivores (Rosenzweig 1966; see also Diamond 1973), (4) gape width and size of the smallest fruit eaten should not be correlated; even minute fruits

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TABLE 1. Fruit diameters, observation times, number of censuses, and bird species recorded at 15 tree species, each observed for at least 4 h at Monteverde, Costa Rica.

Tree species*	Fruit diameter (cm)	Observation time (h)	Number of tree censuses	Number of bird species observed during		
				First 4 h of observation	Total observation time	Total observation time plus censuses
	2.2	26.5	204	3	3	4
	2.3	5.8	316	2	2	5
	1.7	14.0	344	3	3	7
	1.2	6.8	204	3	3	8
	1.8	18.5	848	4	4	5
	1.9	26.0	876	1	3	5
	1.8	6.0	4984	0	0	4
	1.2	37.8	848	4	8	18
	1.7	17.0	316	4	4	5
	2.2	7.0	120		2	4
	1.2	4.6	428		3	5
	1.3	4.0	316	6	6	8
	1.2	23.1	695	5	6	9
	0.8	6.0		5	5	14
	0.6	7.0		6	7	13

\* 13 species in the Lauraceae plus *Hasseltia* (Flacourtiaceae) and *Oreopanax* (Araliaceae).

tend to be conspicuous and easy to capture, unlike minute animal prey. Finally, (5) plants producing small fruits should attract more species of birds than large-fruited plants. Three types of data were used to test these predictions: the sizes of seeds regurgitated by birds versus the sizes of seeds from fruits dropped uneaten by birds; the number of fruit species of a single plant family (Lauraceae) eaten by birds; and the number and sizes of fruit species of all plant families eaten by birds.

#### STUDY SITE AND METHODS

##### *Study area*

For 21 mo between June 1979 and February 1984, I studied fruit-eating birds and fruiting patterns in bird-dispersed plants in the lower montane wet and rain forests of Monteverde, Costa Rica (10°18' N, 84°48' W; Holdridge 1967). The study area (elevation 1350–1550 m) of ≈15 km<sup>2</sup> includes several habitat types maintained by a moisture gradient due to the prevailing northeast trade winds passing over the continental divide (see Lawton and Dryer 1980 for a more complete description of the site). Portions of the undisturbed 2700-ha Monteverde Cloud Forest Preserve, as well as scattered pastures and woodlots, made up the study area.

##### *Determining bird diets*

No single sampling technique could be used to determine the diets of such an ecologically diverse group of fruit-eating birds as occurs at Monteverde. Therefore, I combined various techniques to learn what fruits birds ate. The most thoroughly sampled diets were those of birds that use fixed perches, below which I placed "seed traps" (Snow 1970, Wheelwright 1983).

Seeds from >2500 fruits were recovered beneath calling perches of Three-wattled Bellbirds (*Procnias tricarunculata*), nest-guarding perches of Resplendent Quetzals (*Pharomachrus mocinno*), and courtship branches of Long-tailed Manakins (*Chiroxiphia linearis*). I spent >300 h watching birds feeding at various fruiting trees (including species listed in Table 1; cf. Howe 1977). During the fruiting seasons of 15 species in the Lauraceae, I made weekly 1–4 h morning observations of foraging birds at different individual trees of each species (median = 7.0 h/species). I also conducted separate biweekly censuses of birds at a median of 10 trees per species (Wheelwright 1985; species are listed in Table 1). For each of 28 species in other plant families, I spent 2–8 h/species watching at one or more individual trees during the peak of fruiting, and/or made >20 censuses of various trees on different days during the same period. These species, plus the 15 lauraceous species described above, are here referred to as methodically studied, as opposed to 88 other plant species studied less extensively; for an additional 37 plant species I made only occasional observations. Because this study spanned nearly 5 yr during which various aspects of individual tree species were examined, observation times, census numbers, and sample sizes often differed among plant species. I made additional observations by following flocks for >2000 h in the field. Censuses and miscellaneous observations proved to be more important than watches at trees for recording uncommon or furtive bird species (Table 1; cf. Howe 1977). Various biologists shared additional feeding observations (K. G. Murray, C. Guindon, and R. LaVal, *personal communication*).

Despite the fact that the feeding habits of fruit-eating birds at Monteverde are as well known as those of any

other tropical forest, judging from Snow's (1981) global survey of avian frugivory, the data analyzed here are doubtless incomplete. Much of the original data are presented in Wheelwright et al. (1984), where sampling biases are discussed in detail. Although observation conditions, habitats, and amount of time spent watching at plants were not identical for each species, there were no known systematic biases with regard to fruit size or other traits (except for the Lauraceae; see below), nor were there significant differences in fruit dimensions between groups studied methodically or only casually (Mann-Whitney  $U$  test:  $P > .05$ ,  $n = 43$  and 88 species, respectively).

Fruits rarely require crushing (in contrast to seeds; Willson 1971) or dexterous manipulation (in contrast to fish; Ashmole 1968), but a major problem fruit-eating birds face in eating their food is simply swallowing it. Gape width was, therefore, assumed to determine the upper size limit of food items that can be eaten whole. Esophagus diameter, interclavicular distance, and gizzard volume could also be important limiting factors, but they are difficult or impossible to measure on museum specimens. Gape width, the external distance between commissural points, was measured to within 0.1 mm with calipers on museum specimens of 89 species of fruit-eating birds found at Monteverde (70 of which were observed eating fruits in this study; see Wheelwright et al. 1984). Sample sizes ranged from two (male and female) to nine individuals per species; mean gape width was calculated for each species. Measurements of gape width were 5% narrower for museum specimens of Emerald Toucanets (*Aulacorhynchus prasinus*) than for live birds ( $n = 3$  and 4, respectively), but were similar for prepared and live quetzals ( $n = 4$  and 1, respectively). Gape width was correlated with bill depth and length in nine Monteverde fruit-eating bird species for which I have complete morphological measurements (Spearman rank correlation, width vs. length:  $r_s = 0.80$ ; width vs. depth:  $r_s = 0.78$ ,  $P < .01$ ) (see also Willson 1971).

#### Sampling procedures and fruit measurements

In determining the size distribution of available "bird fruits," I included all plant species whose fruits birds were seen eating as well as all fruits that had characteristics clearly corresponding to van der Pijl's (1969) syndrome of bird fruits: odorless, fleshy fruits, usually persistent on the plant and often brightly colored (see Janson 1983). Fresh fruits were measured to within 0.1 mm with calipers. In this study I focused on fruit diameter as the dimension most likely to be restrictive in "gape-limited" birds, reasoning that relatively long fruits (e.g., *Tetragastris*; Howe 1982) can be swallowed by many bird species if the fruits are not too broad (but see description of *Beilschmiedia costaricensis* below). Pericarp and seeds were weighed to within 0.01 g with a spring balance. Fruits of the Lauraceae were sampled haphazardly from 2 to 25 individual trees per

species. I used a slingshot to propel lead weights attached to monofilament line over 10–30 m high branches. Pulling on the line, I could shake ripe fruits off or break brittle fruit-bearing branches. In two species tested (*Phoebe mexicana* and *Ocotea bernouliana*), fruit and seed dimensions were independent of position in the tree (Mann-Whitney  $U$  test:  $P > .05$ ). Over 2800 fruits and seeds were measured (median = 47 fruits per species).

For most species outside of the Lauraceae, 3–5 representative fruits were selected from one or more plants. Fruits were collected throughout the study by following fruit-eating birds or searching at regular intervals along established transects. In total (counting the Lauraceae), fruits of 246 plant species were measured. To estimate the maximum likely deviation between sample and population means, I measured an average of 51.1 fruits from 2–25 individual plants of each of 15 species. For each species, three fruits were randomly selected using random number tables, and mean values of total mass, net pulp mass, and the ratio of seed mass to fruit mass were compared to values derived from the larger samples from which they were drawn. Average deviations for the three variables from small vs. large samples were 8.4%, 8.6%, and 4.7%, respectively. Measurements of even small samples, therefore, gave a reasonable indication of a species' rank relative to other species. Moreover, sample means for the 246 plant species probably deviated far less from true population means than did the random examples presented above, because I deliberately chose typical fruits (based on knowledge of the range of variability within the population and individual plants). In any event, it is unlikely that the sampling procedure biased the results in any systematic way, because the same procedure was used for fruits of all sizes. This study did not include for consideration birds that eat fruits but destroy most seeds (e.g., parrots) or fruits whose seeds appear to be dispersed mainly by wind, insects, or mammals. Sample sizes vary in different analyses where information was incomplete for certain species. All statistics, except where noted, are nonparametric (Siegel 1956).

## RESULTS

### Fruit sizes and gape widths

Fruits observed to be eaten by birds and those merely presumed to be (e.g., corresponding to van der Pijl's [1969] syndrome of avian seed dispersal) did not differ significantly in fruit diameter (Mann-Whitney  $U$  test:  $P = .39$ ,  $n = 131$  and 115 species, respectively), length ( $P = .26$ ,  $n = 131$  and 115), or mass ( $P = .09$ ,  $n = 114$  and 100), even when the large-fruited Lauraceae were included. Therefore, in the descriptive analyses presented in this section, these samples were combined. Fruits ranged in diameter from 2 to 28 mm (Fig. 1). The majority of plant species (69.1%) had fruits with

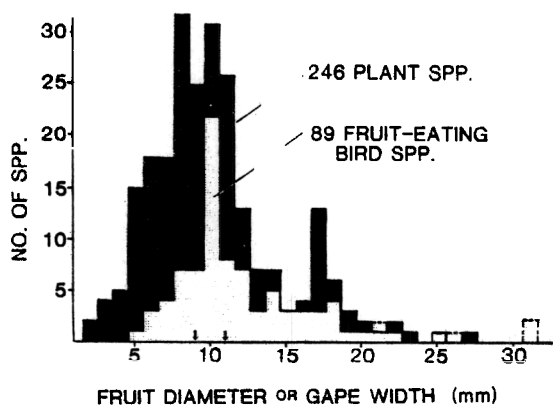


FIG. 1. Frequency distributions of mean diameters of fruits of different species eaten (or presumed eaten; see Methods: Sampling Procedures and Fruit Measurements) by birds (— and ■;  $n = 246$  species) at Monteverde, Costa Rica, and gape widths of co-occurring fruit-eating birds (----- and □;  $n = 89$  species). Medians of distributions indicated by arrows above horizontal axis.

a mean diameter of 5–12 mm; the distribution of fruit diameters showed a second peak near 17 mm. Mean and median fruit diameters were 10.1 mm and 9.0 mm, respectively ( $n = 246$  plant species). Mean and median fruit masses were 1.16 g and 0.46 g, respectively ( $n = 214$ ). Fruit diameter was highly correlated with fruit length ( $n = 246$  species, Spearman rank correlation:  $r_s = 0.88$ ,  $P < .001$ ) and mass ( $n = 214$  species,  $r_s = 0.92$ ,  $P < .001$ ). About half (48.9%) of the species had single-seeded fruits; only 23.8% had more than 10 seeds per fruit. The median ratio of seed mass to fruit mass was 0.21 ( $n = 214$  species). Single-seeded fruits were significantly larger and had greater seed mass to fruit mass ratios than multi-seeded fruits (Mann-Whitney  $U$  test:  $P < .001$ ) (see Wheelwright et al. 1984).

The distribution of gape widths of fruit-eating birds at Monteverde paralleled that of fruit diameters (Fig. 1). The median gape width of 89 bird species was 11 mm, and most bird species had gapes measuring 8–13 mm across. Gape width and fruit diameter distributions were significantly different (Kolmogorov-Smirnov two-sample test:  $P < .01$ ), but their shapes were similar and they did not differ in dispersion or skewness ( $P > .05$ ).

#### Observations within plant species

To test the hypothesis of effective fruit size selectivity by birds, I compared the sizes of seeds regurgitated by birds with seeds from fruits dropped by birds or collected randomly from trees of two species of Lauraceae.

*Beilschmiedia costaricensis* bears bulky black fruits ranging from 17.4 to 25.2 mm in diameter within a single tree. Ripe fruits, irrespective of size, remained on the tree for many months until plucked by an animal. Seed diameter measured 11.7 to 26.7 mm within

the population, and was highly correlated with fruit diameter ( $r_s = 0.92$ ,  $n = 89$ ,  $P < .001$ ). Seed length was correlated with both fruit length ( $r_s = 0.95$ ,  $P < .001$ ) and seed diameter ( $r_s = 0.80$ ,  $P < .001$ ). *B. costaricensis* fruits were far too massive ( $\bar{X} = 12.9$  g) for most birds to handle, but five of the largest bird species, including Emerald Toucanets, fed commonly on them (Wheelwright et al. 1984). Unlike quetzals and bellbirds, toucanets did not habitually return to a specific perch where regurgitated seeds could be sampled using seed traps, so I collected all seeds that I could find regurgitated by a toucanet flock foraging alone at an isolated pasture tree between 3 and 14 January 1981. The diameters of seeds regurgitated (and, by inference, fruits consumed) were smaller than the diameters of seeds from fruits dropped by the birds beneath the tree (Mann-Whitney two-sample test:  $n = 43$  regurgitated seeds and 37 seeds from fruits, most with bill marks, recovered in a complete sample below the tree;  $P < .001$ ; see Fig. 2). The conclusion that toucanets ate smaller fruits than expected is based on the assumptions that, after being swallowed, seeds were not deposited differentially according to size and that the sizes of fruits eaten were correlated with the sizes of seeds regurgitated. Similar results with quetzals and bellbirds (see below) support such assumptions. (At least two reasonable but untested hypotheses argue for differential dispersal according to seed size, with contradictory predictions: [1] large fruits take longer to digest than small fruits [N. Wheelwright, *personal observation*], and therefore their correspondingly large seeds may be carried farther from fruiting trees; [2] birds may tend to remain close to fruiting trees after ingesting large fruits because the seeds of large fruits are especially bulky.)

Seeds of the same species recovered from seed traps beneath quetzal and bellbird perches also reflected an upper size limit to fruits swallowed. The largest regur-

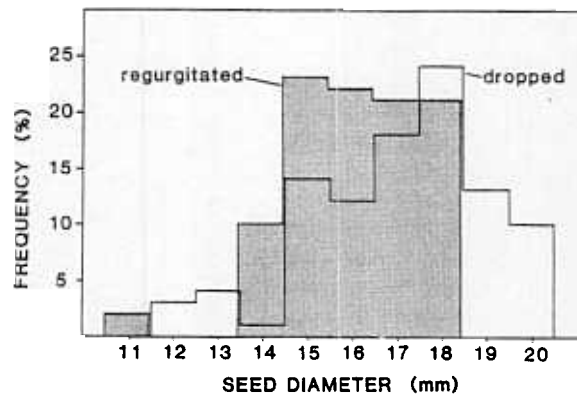


FIG. 2. Frequency distributions of diameters of *Beilschmiedia costaricensis* (Lauraceae) seeds regurgitated below an isolated tree by Emerald Toucanets (*Aulacorhynchus prasinus*) (■;  $n = 43$ ), vs. seed diameters of fruits dropped uneaten by birds below the same tree (□;  $n = 37$ ).

gitated seeds did not exceed 20 mm in diameter for bellbirds or 23 mm for quetzals, as compared to a maximum seed diameter of >26 mm among randomly selected fruits ( $n = 35$  seeds selected, using a random number table, from a larger exhaustive sample of fruits dropped by birds below 10 different *B. costaricensis* trees). Seeds regurgitated by both quetzals and bellbirds were significantly shorter than seeds from the same sample of dropped fruits (quetzals:  $n = 52$  regurgitated seeds; bellbirds:  $n = 19$  regurgitated seeds;  $P < .001$ ), although they were not significantly smaller in diameter ( $P > .05$ ). Quetzals and bellbirds did not differ in the diameters or lengths of *B. costaricensis* seeds regurgitated ( $P > .05$ ). A sample size of 52 *B. costaricensis* seeds is equivalent to a large bird's total fruit consumption over a 3–5 d period. (The fruits take 40–70 min to digest [N. Wheelwright, *personal observation*] and even the larger birds [with the exception of Black Guans, *Chamaepetes unicolor*] can process only one fruit at a time; during a 12-h foraging day, a bird can consume only 10–18 fruits.)

The diameter of *Ocotea tonduzii* fruits (9.7–13.2 mm) was also correlated with seed diameter (4.2–10.4 mm;  $r_s = 0.80$ ,  $n = 199$ ,  $P < .001$ ). Moderate-sized fruits probably pose few handling problems for larger birds but may be too big for small birds such as manakins (gape width 8.5 mm). *Ocotea tonduzii* fruits represented <1% of all fruits eaten by manakins ( $n = 844$ ), so few seeds were recovered from traps suspended beneath male manakin courtship perches. Nonetheless, regurgitated seeds were significantly smaller in diameter than seeds from randomly selected fruits (Mann-Whitney  $U$  two-sample test:  $n = 8$  regurgitated seeds and 38 seeds selected, using a random number table, from a larger sample of fruits taken from 10 different *O. tonduzii* trees;  $P < .001$ ). *O. tonduzii* seeds regurgitated by bellbirds ( $n = 22$ ) were not significantly different in size from the random sample ( $P = .08$ ). Seeds collected in traps beneath two quetzal perches ( $n = 44$ ) were significantly larger than the random sample ( $P < .01$ ), and seeds regurgitated by both bellbirds and quetzals were larger than seeds regurgitated by manakins ( $P < .001$ ). Some effective size selectivity probably occurs simply because birds' nests or perches happen to be located near a large- or small-fruited tree. *O. tonduzii* seeds recovered beneath bellbird ( $n = 22$ ) and quetzal ( $n = 22$ ) perches located only 100 m apart were significantly different in size, and both samples were smaller than those regurgitated by a second quetzal pair ( $n = 22$ ) several hundred metres away (Mann-Whitney  $U$  test:  $P < .01$ ).

#### Observations within a plant family

Another test of the hypothesis that fruit size and gape limitations affect diet is to examine fruit choice by birds among plant species in the same family. Fruit traits such as color and nutrient composition varied little within the Lauraceae, but diameters ranged from 8.0

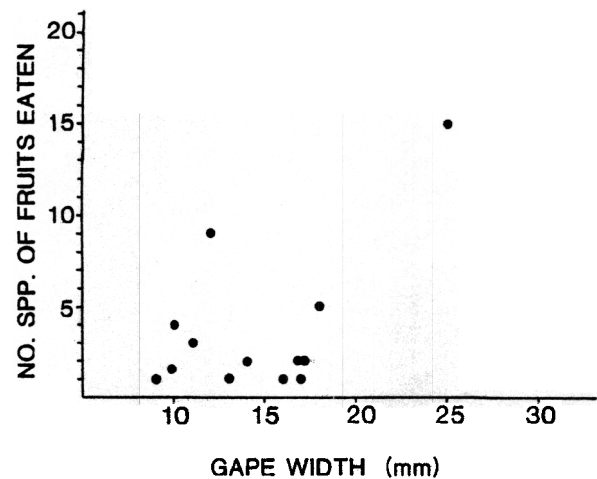


FIG. 3. Gape widths of birds vs. number of species of lauraceous fruits eaten ( $r_s = 0.64$ ,  $n = 17$  bird species,  $P < 0.01$ ; equation of the linear regression:  $Y = 0.6X - 4.8$ ).

mm to 24.8 mm in 23 bird-dispersed species (Wheelwright et al. 1984). By studying a single plant family in detail, I tried to isolate the effects of fruit size while controlling for confounding visual or nutritional traits.

The number of species of lauraceous fruits eaten by a bird species was positively correlated with its gape width (Fig. 3;  $r_s = 0.64$ ,  $n = 17$  bird species,  $P < .01$ ). Toucanets ate fruits of at least 19 of the 23 lauraceous species. Manakins were observed feeding at only 1 species, whereas Mountain Robins fed on 9 species (Wheelwright et al. 1984). The fact that there was no correlation between gape size and frequency of visits to lauraceous trees by 17 bird species (Spearman rank correlation;  $P > .05$ ) indicates that these results are not simply due to the increased conspicuousness or abundance of large-gaped birds, which, in fact, have lower population sizes than most small-gaped fruit-eating birds at Monteverde. Many common species of fruit-eating birds, e.g., manakins, Black-faced Solitaires (*Myadestes melanops*), Olive-striped Flycatchers (*Mionectes olivaceus*), appear rarely if at all at the large-fruited lauraceous trees. During >200 h of systematic tree-watches at all lauraceous species, Mountain Robins accounted for 46.1% of 2337 visits by birds, toucanets 26.4%, quetzals 11.5%, bellbirds 3.6%, and White-throated Robins (*Turdus assimilis*) 2.3%. No other bird species represented >1% of observed visits.

#### Observations among all plant species

The number of fruit species of all plant families included in the diets of 32 well-studied bird species (each with at least five different fruit species recorded eaten [five "fruit records"]), was not significantly correlated with gape width ( $r_s = 0.32$ ,  $P = .09$ ), due in part to the large numbers of fruit species eaten by several small-gaped species, including manakins and Black-faced Solitaires. Large birds tended to eat a broader size range



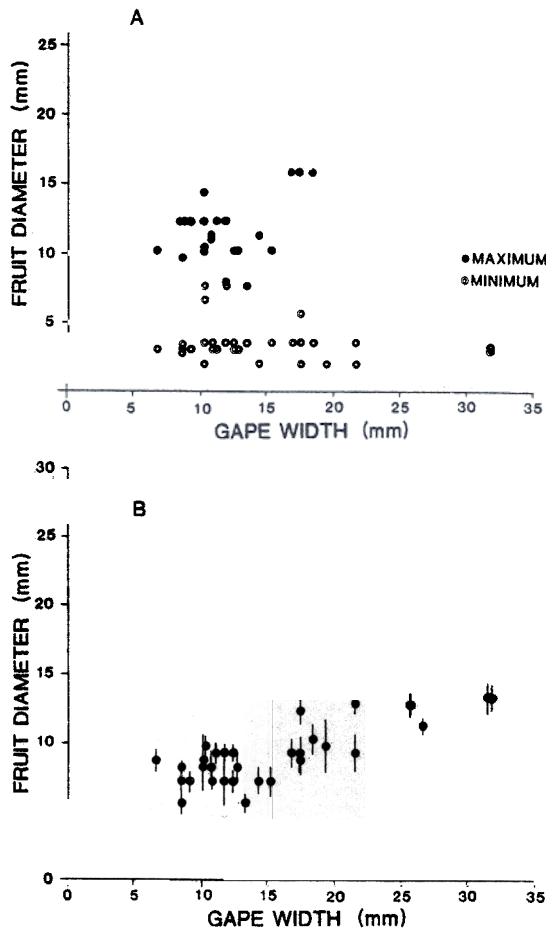


FIG. 4. (A) Maximum and minimum diameters and (B) mean diameter ( $\pm 1$  SD) of fruit species included in the diets of 32 well-studied bird species. In this figure and in Figs. 5–6, it appears that some birds fed on fruits larger than their gapes. Such feeding records are probably due to the fact that birds may feed selectively on small fruits within a plant (i.e., fruits smaller in diameter than the mean values used in these figures). Also, birds can swallow fruits that are slightly wider than their gape because the rami of the mandibles are flexible.

of fruits than small birds, however (Fig. 4). Maximum ( $r_s = 0.53$ ,  $P < .001$ ; Fig. 4A) and mean ( $r_s = 0.61$ ,  $P < .001$ ; Fig. 4B) fruit diameters (as well as lengths and masses:  $P < .001$ ) were also correlated with gape widths for the 32 bird species with five or more feeding records. The slope of the linear regression of maximum fruit diameter and gape width ( $Y = 1.0X + 0.6$ ) reflects the direct relationship between these two variables. On the other hand, gape width was not correlated with diameter of the smallest fruit eaten ( $r_s = -0.10$ ,  $n = 32$  bird species with five or more feeding records;  $P > .05$ ; Fig. 4A) or with length or mass ( $P > .05$ ).

Information on the frequencies of fruit species of different size-classes eaten was available for 10 species of birds studied more intensively (Fig. 5). The diets of

large birds such as toucanets and guans were not disproportionately composed of large fruit species (Fig. 5a–d, Fig. 6; cf. Diamond 1973). Broad-gaped birds frequently fed on the diminutive fruits of *Urera elata* (3 mm) as well as the big drupes of *B. costaricensis*. Below the limit apparently set by gape size, most of the fruit diameter distributions in birds' diets resemble that of the plant community as a whole. However, only in the case of toucanets (Fig. 5d; cf. Fig. 1) was the size distribution of fruits eaten statistically indistinguishable from the distribution of fruit diameters in the plant community (Kolmogorov-Smirnov two-sample test;  $P > .05$ ).

Unbiased data on the relative frequencies of fruits of different sizes eaten by birds are difficult to collect. I have extensive samples for only two species, manakins and bellbirds (Figs. 6 and 7). The size distribution of fruit species eaten was significantly different from the size distribution of individual fruits eaten by bellbirds, which fed disproportionately on medium-sized fruits (Kolmogorov-Smirnov two-sample test;  $P < .01$ ), but this was not so for manakins ( $P > .05$ ).

#### Fruit size and seed dispersal

The number of bird species feeding on the fruits of a particular lauraceous species at Monteverde was inversely correlated with the diameter of the plant's fruits (Fig. 8;  $r_s = -0.71$ ,  $n = 15$  species in the Lauraceae,  $P < .01$ ). At least 17 bird species, representing eight families and four orders, fed on the relatively small fruits of *O. tonduzii*, whereas plant species whose fruits were broader than 17 mm attracted no more than five species of birds (Fig. 8). These results were independent of observation period for plant species observed at least 4 h. For such species, fruit diameter was correlated negatively with the number of bird species recorded during the first 4 h of observation watches ( $r_s = -0.61$ ,  $P < .05$ ; Table 1), the total number recorded during all watches ( $r_s = -0.91$ ,  $P < .01$ ), and the total from all watches plus censuses ( $r_s = -0.74$ ,  $P < .01$ ). There was no correlation between the total number of bird species recorded and either the number of censuses or the total observation time per species ( $r_s = -0.18$  and  $0.04$ , respectively;  $P > .05$ ). Nor was there a correlation between the number of bird species observed during watches alone (i.e., excluding censuses) and the amount of observation time per plant species ( $r_s = 0.18$ ,  $P > .05$ ). Even if such a correlation had been found, the results presented here should not be biased, because neither the amount of observation time nor the number of censuses was correlated with fruit size ( $r_s = 0.13$  and  $0.23$ , respectively;  $P > .05$ ).

Among the 28 additional plant species methodically studied (see Study Site and Methods), small-fruited plant species drew significantly more species of birds than large-fruited species (Fig. 8;  $r_s = -0.51$ ,  $P < .02$ ). When samples for all plant species studied in detail were combined, the correlation was slightly higher

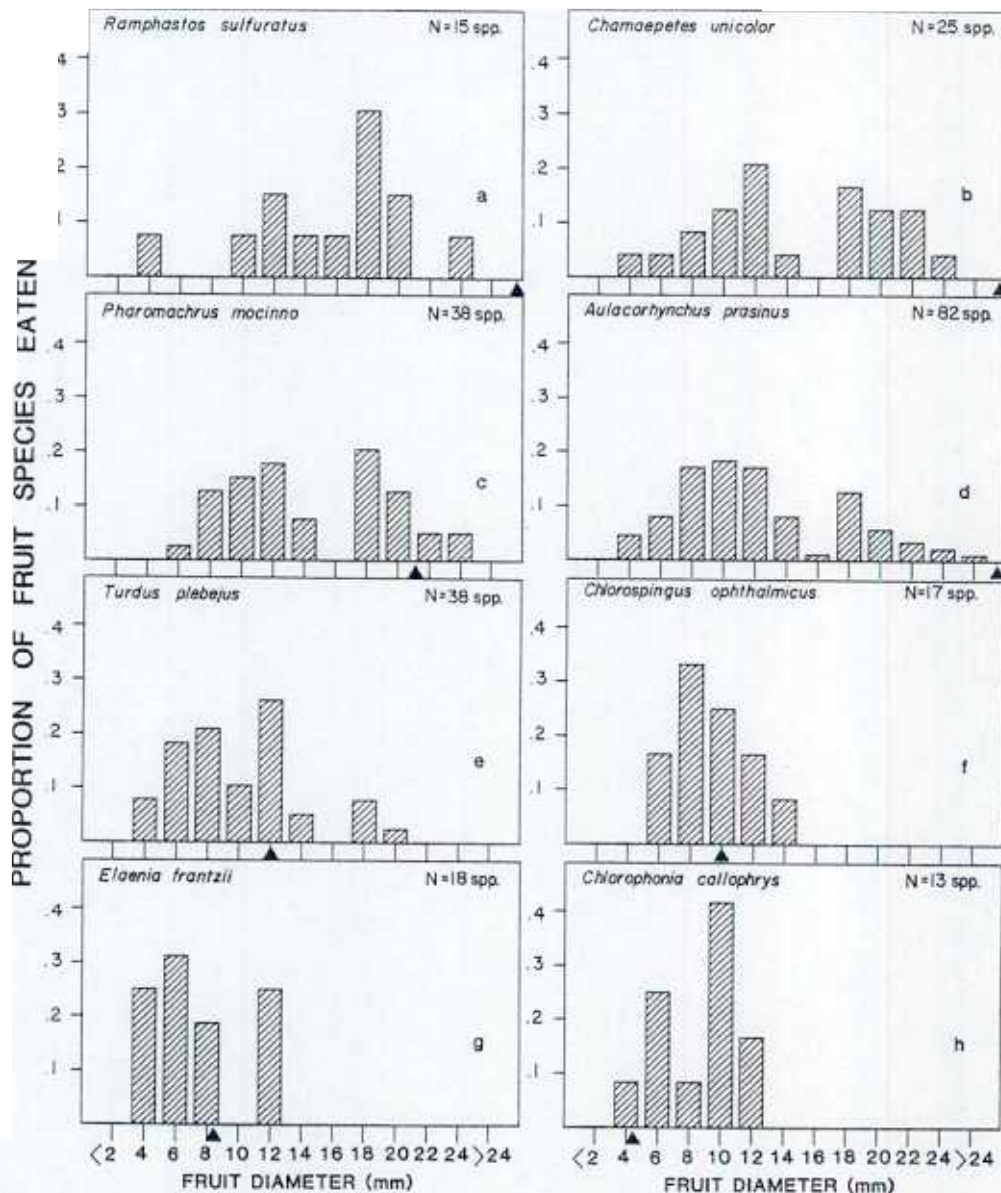


FIG. 5. Frequency distributions of mean diameters of fruit species eaten by birds at Monteverde, Costa Rica: (a) Keel-billed Toucan (*Ramphastos sulfuratus*); (b) Black Guan (*Chamaepetes unicolor*); (c) Resplendent Quetzal (*Pharomachus mocinno*); (d) Emerald Toucanet (*Aulacorhynchus prasinus*); (e) Mountain Robin (*Turdus plebejus*); (f) Common Bush-tanager (*Chlorospingus ophthalmicus*); (g) Mountain Elaenia (*Elaenia frantzii*); (h) Golden-browed Chlorophonia (*Chlorophonia calliphrys*).  $\blacktriangle$  gape widths as measured on museum specimens.

( $r_s = -0.56$ ,  $n = 43$  plant species,  $P < .001$ ). Fruit mass appeared to explain more of the variance ( $r_s = -0.65$ ) than diameter in this case, presumably because it incorporated the constraining effects of both diameter and length (cf. discussion of *B. costaricensis* in Observations within Plant Species, above).

#### DISCUSSION

Seeds collected from seed traps below bellbird, quetzal, and manakin perches, as well as seeds regurgitated by toucanets foraging at an isolated tree, indi-

cated that birds chose among individual fruits on the basis of size. Selective feeding by birds was apparently based less on deliberately choosing small fruits than on indiscriminately plucking fruits and being unable to swallow large ones. Foraging toucanets and other birds commonly plucked large fruits of various species and spent 1–2 min juggling them in their bills in an obvious attempt to swallow them; often they abandoned the effort and dropped the fruits (N. Wheelwright, *personal observation*). Large fruits scarred by bill marks were frequently found below fruiting trees.

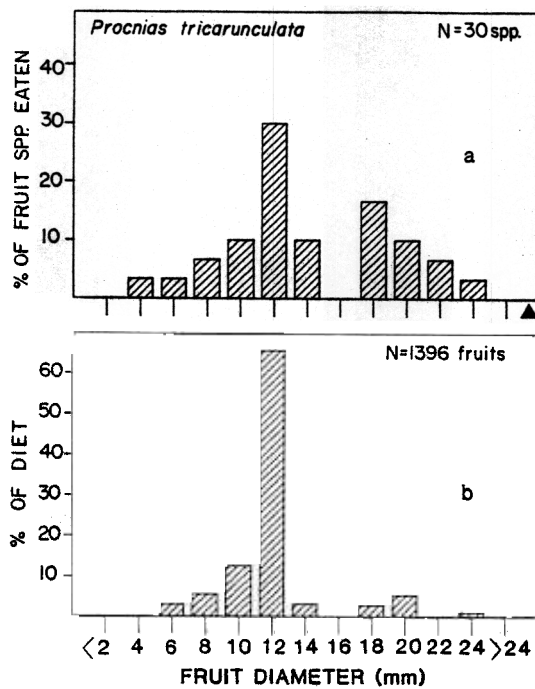


FIG. 6. Frequency distribution of mean diameters of fruit species eaten by Three-wattled Bellbirds (*Procnias tricarunculata*), compared with the size frequencies of individual fruits eaten.  $\blacktriangle$  gape width.

Regardless of the mechanism, the results of size-dependent fruit foraging are likely to be similar from the perspective of the plant. Fruits dropped beneath a plant are hardly more likely to survive than fruits ignored on the tree, unless secondarily disseminated by a terrestrial seed disperser.

Bird species with broad gapes consumed more fruit species in the Lauraceae than did narrow-gaped species. When all fruit species are considered, the positive relationship between gape width and diet breadth was not quite significant for a subsample of well-studied birds (although it was significant for 70 bird species with at least a single feeding record each:  $r_s = 0.34$ ,  $P < .01$ ). Broad-gaped birds tended to eat fruit species of a larger mean and maximum size, and a larger range of sizes. Yet there was no correlation between gape width and minimum fruit size, which suggests that fruit-eating birds differ from more typical predators in their "prey"-size relationship, as discussed below.

#### The sizes of "predators" and "prey"

Carnivores representing different taxa commonly show similar size relationships to their prey. Birds studied include accipiters (Storer 1966), aerial-feeding passerines (Hespenheide 1971), gleaning passerines (Root 1967), sandpipers (Holmes and Pitelka 1968), seed-eating finches (Willson 1971), terns (Ashmole 1968), whelk-feeding corvids (Zach and Smith 1981); other animals studied include alewives (Brooks 1968), bur-

rowing snakes (Seib 1981), carnivorous mammals (Rosenzweig 1966), frogs (Toft 1980), lizards (Schoener and Gorman 1968), plankton-feeding fish (Unger and Lewis 1983), sea snakes (Voris and Moffet 1981), starfish (Paine 1976), stoneflies (Allan 1982). This suggests the following generalizations: (1) the size of the largest prey eaten tends to be directly proportional to the size of the predator; (2) larger predators consume prey of a wider diversity and range of sizes and (3) a larger mean size than do small predators; (4) the size of the smallest prey eaten is usually correlated with predator size, with small prey often underrepresented in, or absent from, the diets of large predators. The slope of the relation between minimum prey size and predator size varies (cf. Schoener 1968, Wilson 1975, Paine 1976, Voris and Moffet 1981). Predators such as baleen whales or anteaters, specialized to feed on clumped, minuscule prey, are notable exceptions.

Interpretations of such patterns, especially lower prey-size limits, derive from foraging theory. Prey that are small relative to a predator are believed to be ignored or taken less often than intermediate-sized prey because the difficulty of detection, capture, and/or handling increases with diminishing prey size (Storer 1966, Root 1967, Recher and Recher 1968, Schoener 1971, Werner and Hall 1974). Upper size limits or preferences tend to be set by the increases in handling time (Sherry and McDade 1982), risk of injury (Bell 1968),

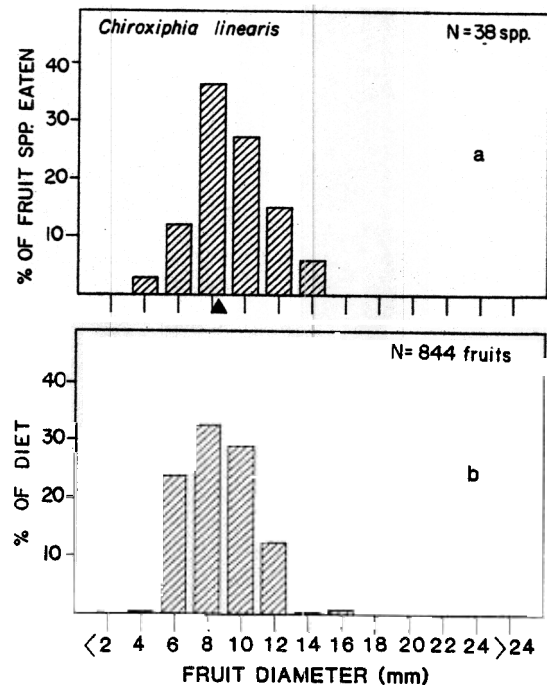


FIG. 7. Frequency distribution of mean diameters of fruit species eaten by Long-tailed Manakins (*Chiroxiphia linearis*), compared with the size frequencies of individual fruits eaten.  $\blacktriangle$  gape width.



or simple physical constraints (Beal and Gillam 1979, Zaret 1980) associated with increasing prey size.

The "prey" of fruit-eating birds differ from the prey of carnivores. Because many plants benefit by having their seeds disseminated (Ridley 1930, van der Pijl 1969, Howe and Smallwood 1982), most fruits whose seeds are dispersed by birds are not difficult to detect or handle (Snow 1971, Wheelwright 1983). Even diminutive fruits are typically easy to find because they may be brightly colored, aggregated into a conspicuous cluster or compound fruit, or set off against contrastingly colored associated structures, such as leaves, enlarged bracts, or pedicels (Stiles 1982, Wheelwright and Janson 1985). Despite their size, small fruits are no harder to capture than large fruits; unlike most animal prey, fruits are sessile, non-elusive, and relatively undefended (Snow 1971; but see Herrera 1982).

The hypothesis that fruit-eating birds differ from carnivores in the relationship between body size and food size is suggested by the lack of correlation between bird gape width and the minimum size of fruits consumed, and by the frequency with which large-gaped birds at Monteverde eat very small fruits. This hypothesis would be supported if the slope of the relationship between body size and minimum "prey" size were shown to be low for these birds, relative to that for typical carnivores. A review of the foraging literature indicates that this is true in most cases, but not in all. For example, Wilson's (1975) general conclusion, based on data in Craighead and Craighead (1956) (see also Storer 1966), that "minimum prey size . . . hardly changes over a wide range of predator sizes" is weakened by a closer inspection of the data, particularly when raptors are considered by ecological group. Owls, accipiters, falcons, and soaring hawks all display an increase in minimum prey size with body size. The same holds for many other birds (Ashmole 1968, Smith and Temple 1982), most other predators cited by Wilson (1975), and some, but apparently not all seed-eating birds (Newton 1967; but see Willson 1971, Rosenberg et al. 1982).

#### *Consequences for seed dispersal*

This study suggests that, by producing large fruits, plants unavoidably exclude narrow-gaped birds and reduce the number of potential dispersers of their seeds. McKey (1975) and Howe and Estabrook (1977) have proposed that the evolution of fruit size is at least partly determined by the benefits a plant gains by limiting its dispersers to a restricted set of reliable, specialized birds. An alternative hypothesis is that fruit size depends upon seed size, which in turn is determined by the need to store energy and nutrients for seedling establishment following dispersal (Snow 1971). According to the latter view, large-fruited plants (with correspondingly large seeds) are actually at a disadvantage with respect to dispersal (Wheelwright and Orians 1982), in contrast to the view of McKey (1975). "Escape in size" (Paine

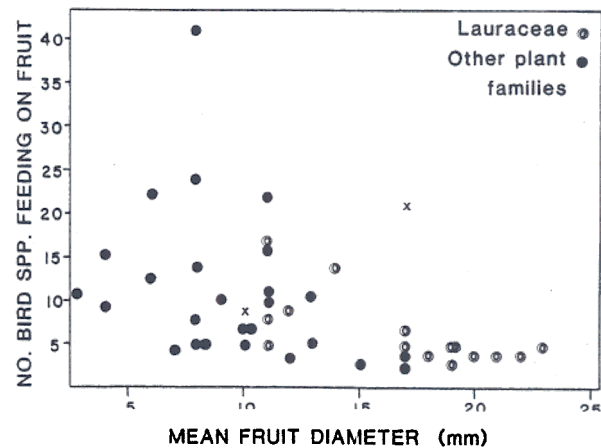


FIG. 8. Number of bird species observed feeding on fruits of different plant species as a function of mean fruit diameter. ○ 15 species in the Lauraceae. ● 28 species from other families that were also studied systematically. × indicates two *Ficus* species whose fruits were eaten piecemeal (not included in analyses).

1976), which is an advantage for most prey, may be a liability for fruits because of poorer dispersal. Large fruits are more likely to attract fewer seed dispersers and to be dropped uneaten beneath the tree, where survival prospects are low. These costs are presumably offset by the competitive advantages gained by the seedlings having greater reserves in large seeds (Howe and Richter 1982). Size constraints also affect the symmetry of interactions between plants and the birds that disperse their seeds: large-fruited plants, which are the most specialized in terms of potential seed dispersers, must depend on broad-gaped birds, which are the most generalized in terms of fruit diet.

Although size is demonstrably a key characteristic of fruits, it does not explain the wide variability in the number of bird species feeding at different plant species that have fruits of the same size (Fig. 8). Part of the variance is due to sampling biases but the variability also presumably reflects discrimination by birds based on other fruit attributes. Color showed no consistent relation to fruit size in the same plant species (Wheelwright and Janson 1985), and there was no indication that nutrient composition was strongly tied to size (Wheelwright et al. 1984; but see Herrera 1981). Concentrations of N, Mg, K, lipids, and total nonstructural carbohydrates were not correlated with fruit mass in 23 Monteverde lauraceous species or in 11 other bird-dispersed species for which I have nutritional data (Spearman rank correlation;  $P > .05$ ). Plant growth form, commonness, and fecundity, however, unquestionably influence the number of potential seed dispersers for a plant (Wheelwright et al. 1984). The subtle effects of many fruit traits in combination will be essential in understanding the foraging behavior of fruit-eating birds and their coevolution with bird-dispersed

plants. Without adequately controlling first for the effect of fruit size, however, it will be difficult to establish whether birds ignore fruits because they are insufficiently nutritious, or simply too big to eat.

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