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FEEDING METHODS AND EFFICIENCIES OF SELECTED FRUGIVOROUS BIRDS[1]

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Abstract. I report on handling methods and efficiencies of 26 species of Paraguayan birds feeding on fruits of *Allophyllus edulis* (Sapindaceae). A bird may swallow fruits whole (Type I: pluck and swallow feeders), hold a fruit and cut the pulp from the seed with the edge of the bill, swallowing the pulp but not the seed (Type II: cut or mash feeders), or take bites of pulp from a fruit that hangs from the tree or that is held and manipulated against a branch (Type III: push and bite feeders). In terms of absolute amount of pulp obtained from a fruit, and amount obtained per unit time, Type I species are far more efficient than Type II and III species. Bill morphology influences feeding methods but is not the only important factor. Diet breadth does not appear to be significant. Consideration of feeding efficiency relative to the needs of the birds indicates that these species need to spend relatively little time feeding to meet their estimated energetic needs, and that handling time has a relatively trivial effect on the time/energy budgets of the bird species observed.

Key words: Allophyllus edulis; *bill morphology; existence energy; feeding efficiency; frugivory; generalist; handling time; Paraguay; specialist.*

INTRODUCTION

Numerous authors have documented the use of fruits of single species of plants by many species of birds (Eisenmann 1961, Land 1963, Diamond and Terborgh 1967, Terborgh and Diamond 1970, McDiarmid et al. 1977, Wheelwright et al. 1984). The bird species feeding on a particular tree often represent a wide taxonomic array and exhibit great morphological and trophic diversity. Not surprisingly, they feed on the same fruits in different ways, presumably with varying efficiencies. Although some feeding methods have been described, they have been evaluated primarily with regard to their impact on seed dispersal (Brockelman 1982, Trainer and Will 1984, Moermond and Denslow 1985). Little is known about feeding efficiency or its significance for the birds. Recent work in Paraguay with *Allophyllus edulis,* a tree with bird-dispersed seeds, has provided an opportunity to examine feeding methods and efficiency. Seed dispersal will be considered in detail elsewhere (Foster, unpubl. data).

At least 26 species of birds representing nine families or subfamilies and ranging in size from about 13 to 375 g eat fruits of *Allophyllus edulis* (St. Hil.) Radlk. (Sapindaceae) in Paraguay. The birds include species that are primarily frugivorous, eat large quantities of both fruit and insects, or are omnivorous. In this paper, I describe the ways in which these birds feed on *Allophyllus* fruit, and their feeding efficiency in terms of (1) the rate at which pulp is ingested (exocarp plus mesocarp acquired per unit time), and (2) the absolute amount of pulp ingested, per fruit, regardless of time expended. I also provide data on diets. By comparing the species, it may be possible to identify ways in which body size, bill dimensions, and feeding behavior influence efficiency. The significance of feeding efficiency can then be evaluated through a consideration of the birds' energy requirements and the energy supplied by the fruits.

METHODS

The study was conducted at El Tirol (ca. 55°47′W, 27°11′S), Dpto. Itapóa, Paraguay during the *A. edulis* fruiting seasons of 1980 to 1983, with limited observations also made in 1976, 1978, and 1979. This species, locally known as Cocú, is found in low densities in relatively undisturbed forest, at high densities in second growth forest, and as an occasional shade tree in areas cleared for cultivation (Foster, unpubl. data). Trees may reach heights of 18 m, but rarely exceed 12 m.

Allophyllus fruits are drupes borne on racemes throughout the tree. In any given year, the fruit crop may range from 500 to >30,000 on different trees (Foster, unpubl. data). Fruiting is highly

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FIGURE 1. A branch of *Allophyllus edulis* with racemes of ripe and ripening fruits.

synchronized within and between trees. Ripe fruits usually are available for 4 to 5 weeks between mid-September and the end of October, with a fruiting peak lasting about 3 weeks. Ripe fruits (Fig. 1) are red and range from ca. 6.7 to 9.4 mm long by 6.6 to 9.6 mm in diameter (Foster, unpubl. data). The fruit has a thin exocarp and a sweet, juicy, fleshy mesocarp, and contains a single drop-shaped seed ranging from ca. 5.0 to 7.0 mm long and from 3.9 to 5.4 mm in diameter.

Birds eating *A. edulis* fruits were observed in the wild. Detailed notes were taken on the methods of feeding, and handling times for individual fruits were recorded with a stopwatch. In addition, birds of nine of these species were mist-netted and maintained in fiberglass screen cages (1.0 × 0.75 × 1.0 m high, with one crosswise and one lengthwise horizontal perch) where they were presented with *Allophyllus* fruits suspended from fine wires. Feeding behavior was observed, handling time was recorded, and the amount of pulp actually swallowed was determined. The percentage of the available pulp that this represented was calculated as indicated in Table 1, as a measure of efficiency of pulp removal.

Handling times per fruit were recorded from the time the bird first touched a fruit until it either swallowed or dropped the seed. The amount of fruit pulp consumed per unit time, a second measure of efficiency, was calculated using average handling times and average amounts of pulp swallowed per fruit.

Birds were held in cloth net cages (28 cm diameter × 38 cm high) in the dark for 1 to 2 hr prior to testing or between trials. If a bird had not begun to eat after 30 min in the test cage, the trial was terminated. Each bird was used for a maximum of two trials, with the exception of two *Turdus rufiventris* that were used for three trials each.

TABLE 1. Methods of calculating pulp ingested.

Step 1.	Weight of 20 whole fruits, = A
Step 2.	Weight of whole fruits not consumed during the feeding trial, = B
Step 3.	Weight of whole fruits consumed during the feeding trial, A − B = C
Step 4.	Weight of seeds (recovered*) and unswallowed pulp, = D
Step 5.	Weight of pulp actually consumed, C − D = E
Step 6.	Weight of cleaned seeds from eaten fruits, = F
Step 7.	Weight of total pulp from eaten fruits, C − F = G
Step 8.	Weight of pulp eaten per fruit, G ÷ number fruits eaten = P_w
Step 9.	Percent of pulp available on fruit that was swallowed, E ÷ G × 100 = $P_{\%}$

* At the end of a trial, the bird was held in a small cloth cage until all seeds swallowed were either defecated or regurgitated. These were collected along with all pulp material dropped by the bird on the perch, floor, or walls of the cage. Forceps and preweighed, absorbent filter paper were used so that fruit juices as well as solid matter, could be recovered.

Spring balances and calipers were used to weigh and measure (to the nearest 0.1 mm) 403 birds netted or collected at Tirol and 19 taken at three other localities in eastern Paraguay. Bill length was measured from the nostril to the tip of the bill, rictal width (= gape width of Wheelwright 1985) at the level of the rictal commissure. Bill gape, the distance on an open bill from the tip of the upper mandible to the tip of the lower mandible, was measured only on live or freshly dead specimens. To approximate the maximum natural gape, I placed my thumbs on the frontoparietal area at the back of the skull and exerted dorsal pressure with my index fingers on the retroarticular processes of the lower jaw. This depressed the lower jaw, and protracted the quadrates, raising the upper jaw (R. Zusi, pers. comm.). The bill opened to a point at which the rictal commissures were extended, but maintained a slight, posteriorly directed concavity. No unnatural stretching of the commissures was apparent. However, because degree of opening may be influenced by the way in which the pressure is applied, maximum and minimum values were discarded for species with sample sizes of three or more. Bill gape data for all individuals within a species were combined because sample sizes were small and because data were taken from many unsexed birds.

TABLE 2. Species of birds that eat *Allophyllus edulis*: diets, fruit handling methods, and weights.[1]

Species	Trophic type[2]	$\bar{x}$ Weight[3] (g) ♂♂, ♀♀	Species	Trophic type[2]	$\bar{x}$ Weight[3] (g) ♂♂, ♀♀
		Type I			
A:			B. cont'd.		
Pyroderus scutatus	F	375, 330	*Myiodynastes maculatus*	I/F	44, 51
Cyanocorax chrysops	O	157, 159	*Thraupis sayaca*	I/F	31, 33
Cacicus haemorrhous	I/F	102, –	*Empidonomus varius*	I/F	27, 27
Pitangus sulphuratus	O	63, 66	*Chiroxiphia caudata*	F	23, 23
B:			*Zonotrichia capensis*	O	20, 20
Turdus rufiventris	I/F	67, 72	*Vireo olivaceus*	I/f	15, 15
Turdus leucomelas	I/F	70, 67	*Elaenia parvirostris*	I/F	16, 18
Turdus amaurochalinus	I/F	63, 63	*Elaenia albiceps*	I/F	16, 15
		Type II			
Tachyphonus cornatus	I/f	26, 27	*Trichothraupis melanops*	I/f	20, 22
		Type III			
Tangara seledon	F/i	19, 21	*Chlorophonia cyanea*	F	14, 15
Dacnis cayana	F	16, 16	*Euphonia pectoralis*	F	14, 14
Coryphospingus cucullatus	O	15, 15	*Hemithraupis guira*	I/f	13, 14
Euphonia violacea	F	14, 15	*Euphonia chlorotica*	F	12, 13

[1] *Mionectes rufiventris*, feeding type undetermined, I/F, ♂♂ = 14 g, ♀♀ = 12 g.
[2] F = Primarily frugivorous; F/I = eating large quantities of fruit and insects; F/i = eating large quantities of fruit and lesser amounts of insects; I/f = eating large quantities of insects and lesser amounts of fruit; O = omnivorous. See Appendix for detailed information.
[3] See Appendix for more precise means, sample sizes, and standard deviations.

Trophic designations for bird species were based on my observations of foraging behavior at Tirol, examination of stomach contents, and reports in the literature. For several species available information is limited. In addition diets of some species change seasonally, and stomach samples may be biased since specimens are not always collected at random. Nevertheless, because the diet categories used are broad, it is unlikely that these factors will significantly influence the results of the analysis. Birds whose diets are two-thirds fruit were considered to be primarily frugivorous, while those in which fruit (or insects) constituted from one- to two-thirds of the diet were assumed to eat large quantities of both fruit and insects. Birds exploiting at least three major classes of food (e.g., fruit, insects, vertebrates, seeds) were designated as omnivores.

Nutrient content of the fruit pulp was determined, and metabolizable energy content estimated, as outlined in Foster (1977). Metabolizable energy was calculated *only* on the basis of the presumed edible portions of the pulp: lipid, soluble carbohydrate, and protein, with corrections for excretion of nitrogen in organic form (Ricklefs 1974). Nevertheless, even edible portions are not totally digestible. Therefore, digestive efficiency (assimilated energy/gross energy intake) of this portion was set at 90% (=ca. 77% efficiency for all fruit pulp). This is an arbitrary figure, given our lack of knowledge of birds' abilities to assimilate nutrients. However, some empirical data support such an estimate (Martin 1968, Fisher 1972).

Basal metabolic rate (BMR) was calculated with the equation,

$$\text{BMR kcal/day} = 24 \times 4.78\,W^{0.726}$$

where W is body weight in kg (King 1974). Energy requirements for daily existence (DEE) were arbitrarily calculated as 1.5 BMR, those for maintenance of social interactions (DSE) as 2.5 BMR, and those for reproduction (DRE) as 4.0 BMR (see discussion in King 1974). These values probably overestimate energy requirements, particularly for species weighing more than 50 g.

RESULTS

FEEDING BEHAVIOR

Fruit handling. Handling behavior exhibited by birds feeding on *A. edulis* generally may be assigned to one of three types, described below. Idiosyncracies of feeding behavior typical of individual species are summarized in the Appendix, together with detailed data on weights, stomach contents, and diet.

Type I (pluck and swallow feeders): The fruit is plucked and swallowed whole; usually birds require only a few seconds or less to manipulate the fruit from the tip of the bill to the back of the throat. Birds tip their heads upward, opening the bill so the fruit rolls backward, or they rapidly open the bill and move the head forward, grabbing the fruit again deeper in the bill. The fruit moves to the muscular stomach where the pulp is removed. The seeds are regurgitated or passed through the intestine, depending upon the bird species; some species do both (see Appendix). Birds of different species may perch, reach, and pluck a fruit, hover and grab one, or make a "fruit-catching" sally, flying by a fruit and snatching it.

Larger species in this category (Type IA, Table 2) generally perch and grab, removing several to many fruits simultaneously. Smaller species (Type IB, Table 2) pluck and swallow one fruit at a time, although additional fruits may be swallowed immediately, before seeds from the first few are eliminated.

Type II (cut or mash feeders): Although details vary among species, the basic pattern is for a bird feeding by this method (Table 2) to grasp the fruit in the tip of its bill, the upper mandible often impaling or sinking into the pulp. The bird then rolls the fruit in its bill with the lower mandible and the tongue, cutting the pulp from the seed with the tomium of the upper mandible. A long string of pulp trails below the bill, or a wad piles on top of it before the pulp is pulled back to the mouth with the tongue and swallowed. Ultimately, the seed shoots out the end of the bill and is dropped, is spit out, or works its way to the face or top of the bill so that the bird must shake it off or wipe it onto a branch. Sometimes the pulp is not cleanly cut but rather is pressed and squashed away from the seed (="mashing" of Moermond 1983 and Moermond and Denslow 1985). Feeding is messy; pieces of pulp are dropped or remain stuck to the perch, the bird's bill and face.

Type III (push and bite feeders): Several types of feeding behavior are combined in this category because they all involve removal of the pulp or the manipulation of the fruit with the assistance of some structure other than the bill. For example, some Type III species (Table 2) often do not pluck the fruit but simply take bites from it as it remains attached to and supported by the pedicel. In this case the birds frequently move to a new fruit after a few bites although considerable pulp may remain around the seed. The most common method of feeding is for the bird to pluck a fruit, often impaling it on the upper mandible, carry it immediately to a horizontal perch, and then roll, bite, or otherwise manipulate it while pushing it against the branch. Often the fruit stays on the branch while the bird takes a series of small bites. At other times, the bird retains the fruit in its bill but turns and manipulates it to cut off the pulp by pushing the fruit against the branch. With this type of feeding a great deal of pulp is scattered about; pieces are left on the perch and adhere to the bird's face.

The cut or mash (Type II), and push and bite (Type III) feeding methods grade into one another, since birds in category III sometimes manipulate fruit in their bills without use of a branch. In this case they repeatedly mash the fruit by opening and closing their bills on it, removing pieces of pulp and ultimately dropping the seed (see Moermond and Denslow 1985 for a similar description of feeding in several emberizids). Some species turn the fruit in their bills, cutting the pulp free and swallowing it. They are less adept at this than birds in category II, however, being unable to open their bills sufficiently to encompass the entire fruit freely. Generally the birds do not remove the pulp in a single string, but scatter it widely.

Species observed eating *A. edulis* were assigned to a feeding category (Table 2), with the exception of *Mionectes rufiventris,* for which feeding type was not determined. Most species used only one feeding method, although a few occasionally used two (e.g., *Tachyphonus coronatus, Trichothraupis melanops;* see Appendix). *Thraupis sayaca,* in contrast, handled *Allophyllus* fruits in all three ways.

Aggression. During more than 140 hr of observation of birds feeding in 10 *Allophyllus* trees, only two instances of interspecific and ca. seven of intraspecific aggression were observed. One male *T. melanops* who closely approached another was chased to a different perch in the tree. All other interactions involved male *Euphonia violacea.* One individual was chased from the tree by a *Dacnis cayana.* Another displaced a *Chlorophonia cyanea* with a short chase within the tree. The latter *E. violacea* also twice chased the same conspecific male from the tree. Finally, four males feeding at the same time exhibited some agonistic behavior, supplanting and chasing briefly within the tree. This occurred when males were within ca. 75 cm of each other.

Length of visit. For many of the species it was difficult to identify discrete foraging bouts. Birds variously preened, sang, perched quietly, or flew around within the tree, before, during, or after feeding (including fruit examination). Nevertheless, to obtain some measure of the time that a bird spent in an *Allophyllus* tree, I determined for each fruit handling category, the median length of visits by individual birds of all species. Values were extremely variable both within and between species, but showed a consistent trend. Visits by Type I birds ranged from 1 to 300 sec (n = 60, median = 30 sec), and those of Type II birds, from 8 to 180 sec (n = 18, median = 40 sec). Type III birds made considerably longer visits to *Allophyllus* (median = 150 sec, n = 71, range = 20–1,200 sec). When values were controlled for bird size (visit length ÷ maximum weight for the species from Table 2), median visit lengths showed the same trend: Type I = 0.74 sec/g body weight; Type II = 1.55; Type III = 9.231.

FORAGING EFFICIENCY

In my cage experiments, the percentage of pulp that was actually consumed of the total available on a fruit ranged from 19.3 to 99.9% (Table 3). Type I birds were the most efficient, consistently ingesting 97% or more. The ranges of efficiency of pulp ingestion by Type II and Type III feeders overlapped substantially, although the average value for *T. coronatus* far exceeded those for the rest (Table 3).

Pulp intake per unit time also was associated with handling method. All Type I species were significantly more efficient than Type II species, both *Turdus* significantly more efficient than all Type III species, and *C. caudata* more efficient than *E. violacea* (ANOVA, $F_{[8, 65]} = 92.76$, $P \leq 0.001$; Tukey-Kramer Means Test, $Q_{[9, 65]} = 5.3442$, $P \leq 0.01$). The lack of significant differences in other species comparisons likely reflects small samples for Type III species. Even when related to bird size, feeding rates in the Type I mode greatly exceeded those in the Type II and Type III modes (Table 3).

BIRD DIETS AND MORPHOLOGY

The species feeding according to Type III methods are generally frugivorous (Table 2, Appendix). Those exhibiting Type II methods eat large quantities of both fruit and insects, and those exhibiting Type I feeding are primarily frugivorous, eat large quantities of both fruit and insects, or are omnivorous.

Type II and III birds tend to be small (Table 2, Appendix), although Type II species are consistently larger than Type III species. Birds of all sizes were represented among those using Type I methods. Average bill dimensions of Type I birds overlapped considerably with those of Type II forms (Table 4). Bill dimensions of Type III birds were consistently smaller, although they showed some overlap with those of Type I and Type II birds.

ENERGY REQUIREMENTS AND FRUIT CONTENTS

The metabolizable energy in the pulp (exocarp + mesocarp) of an average ripe fruit of *A. edulis* was calculated as 0.23 kcal, or 0.96 kJ (n = 13 trees, r = 0.079 to 0.300 kcal, SD = 0.058). Protein content of pulp averaged 5.66% (n = 13 trees, r = 3.66 to 9.29%, SD = 1.65).

Daily existence energy requirements ranged from ca. 7 to 11 kcal/day for Type III birds (12 to 21 g), from ca. 11 to 13 kcal/day for Type II birds (20 to 27 g), and from ca. 23 to 85 and 8 to 26 kcal/day for Type IA (63 to 375 g) and Type IB (15 to 72 g) birds, respectively. Energy requirements for socially active and breeding birds would be approximately 1.67 and 2.67 times these values. The number of fruits a bird would have to eat to meet these requirements depends not only on the fruit nutrient content but also on the bird's efficiency at consuming and assimilating the pulp. For the nine species for which I have efficiency data, I calculated the number of fruits as well as an estimated daily feeding time required to meet daily existence energy requirements on a diet consisting only of *A. edulis* (Table 5).

The estimated DDE for the Type I-feeding *Turdus* is about twice that of Type II feeders and three times that for the Type III feeders, but the number of *Allophyllus* fruits these thrushes would need to consume to meet these needs are only ca. 1.3 to 1.5, and 1.1 to 1.9 times more, respectively. In contrast, the time needed by the thrushes for feeding is only about 6 to 11% of that required by the Type II feeders, and only 4 to 9% of that required by Type III birds. *Chiroxiphia,* whose energy requirements approximate those of the Type II feeders, would eat 28

TABLE 3. Average feeding efficiencies of birds consuming fruits of *Allophyllus edulis.*

	Pulp eaten/fruit (g)	Pulp eaten/fruit (%)	Handling time/fruit (sec)	Feeding rate (g/sec)	Feeding rate (g/sec/g body wt.)[1]
			Type I		
Turdus rufiventris					
Range	0.266–0.581	97.0–99.9	0.10–2.5		
$\bar{x}$	0.340	99.05	0.92	0.370	51.4×10^{-4}
SD (n)[2]	0.092 (12)	(12)	0.315 (82)		
Turdus leucomelas					
Range	0.168–0.300	98.0–99.4	0.20–1.5		
$\bar{x}$	0.252	98.78	1.08	0.235	33.5×10^{-4}
SD (n)	0.049 (6)	(6)	0.392 (16)		
Chiroxiphia caudata					
Range	0.237–0.347	97.1–99.2	0.75–7.6		
$\bar{x}$	0.293	98.41	2.5	0.116	50.5×10^{-4}
SD (n)	0.044 (6)	(6)	1.72 (27)		
			Type II		
Tachyphonus coronatus					
Range	0.131–0.331	38.6–91.0	8.0–57.0		
$\bar{x}$	0.259	76.08	23.4	0.011	4.1×10^{-4}
SD (n)	0.056 (13)	(13)	9.69 (65)		
Trichothraupis melanops					
Range	0.086–0.228	19.3–77.9	4.0–56.5		
$\bar{x}$	0.161	54.99	16.1	0.010	4.5×10^{-4}
SD (n)	0.043 (24)	(24)	8.77 (103)		
			Type III		
Euphonia chlorotica					
Range	0.188–0.193	51.9–63.9	10.0–43.0		
$\bar{x}$	0.191	57.89	31.4	0.006	4.7×10^{-4}
SD (n)	0.004 (2)	(2)	11.99 (10)		
Euphonia violacea					
Range	0.105–0.285	32.1–86.7	8.0–64.0		
$\bar{x}$	0.183	56.30	31.6	0.006	3.9×10^{-4}
SD (n)	0.064 (6)	(6)	14.14 (24)		
Euphonia pectoralis					
Range	0.092–0.282	41.9–68.2	39.0–47.0		
$\bar{x}$	0.187	55.03	42.3	0.004	3.2×10^{-4}
SD (n)	0.135 (2)	(2)	4.16 (3)		
Hemithraupis guira					
Range	0.050–0.124	20.9–43.8	8.0–52.5		
$\bar{x}$	0.097	35.87	28.0	0.004	2.5×10^{-4}
SD (n)	0.041 (3)	(3)	18.41 (11)		

[1] Feeding rate in g/sec (from column 4) ÷ the greatest body weight for the species from Table 2.
[2] n = Number of trials.

to 38% fewer fruits in about 10% of the time. The estimated energy demands of this species exceed those of the Type III species by 33 to 50%. Nevertheless, the fruits required range from 12 to 45% fewer, eaten in 6 to 8% of the time. The estimated energetic needs of the Type II species are ca. 1.2 to 1.6 those of the Type III species. However, the Type II birds should require from 0.77 to 1.4 times the fruits, which would be eaten in roughly 53 to 92% of the time. When the feeding categories are compared with regard to feeding time per gram body weight, Type I feeders are again the most efficient, followed by Type II and Type III birds (Table 5). *Chiroxiphia caudata* and *Trichothraupis melanops,* for example, are birds of approximately equal weight. Yet *C. caudata,* a Type I species, should require only 0.13 min/g body weight to

TABLE 4. Bill dimensions (mm) of bird species feeding on *Allophyllus edulis*.[1]

Species	Length $\bar{x} \pm$ SD, *n*	Width at rictal commissure $\bar{x} \pm$ SD, *n*	Gape at tip $\bar{x} \pm$ SD, (*n*)
	Type I		
Pyroderus scutatus	27.70, 1♂ —	30.85, 1 ♂ 25.30, 1 ♀	—
Cyanocorax chrysops	22.10 ± 0.42, 2 ♂♂ 21.54 ± 0.65, 8 ♀♀	18.55 ± 1.63, 2 ♂♂ 17.74 ± 0.78, 8 ♀♀	—
Cacicus haemorrhous	23.58 ± 0.82, 5 ♂♂	13.23 ± 0.67, 6 ♂♂	—
Pitangus sulphuratus	23.38 ± 1.25, 4 ♂♂ 22.91 ± 1.27, 6 ♀♀	15.80 ± 1.07, 4 ♂♂ 16.75 ± 0.42, 6 ♀♀	—
Turdus rufiventris	14.81 ± 0.63, 11 ♂♂ 14.40 ± 0.67, 8 ♀♀	12.66 ± 0.81, 11 ♂♂ 13.84 ± 0.96, 9 ♀♀	24.27 ± 1.77 (7)
Turdus leucomelas	13.37 ± 0.82, 9 ♂♂ 13.14 ± 0.29, 6 ♀♀	13.44 ± 0.84, 8 ♂♂ 14.40 ± 0.70, 5 ♀♀	20.40 ± 0.57 (2)
Turdus amaurochalinus	13.22 ± 0.79, 4 ♂♂ 13.24 ± 0.89, 3 ♀♀	12.90 ± 0.40, 4 ♂♂ 11.67 ± 0.95, 3 ♀♀	26.0 (1)
Thraupis sayaca	9.52 ± 0.29, 4 ♂♂ 9.72 ± 0.46, 9 ♀♀	10.19 ± 1.10, 4 ♂♂ 10.53 ± 0.97, 9 ♀♀	—
Myiodynastes maculatus	17.64 ± 0.95, 6 ♂♂ 18.11 ± 0.91, 2 ♀♀	14.90 ± 1.03, 6 ♂♂ 14.90 ± 0.14, 2 ♀♀	—
Empidonomus varius	10.33 ± 0.55, 9 ♂♂ 10.06, 1 ♀	12.46 ± 0.79, 9 ♂♂ 12.70, 1 ♀	—
Chiroxiphia caudata	6.22 ± 0.22, 21 ♂♂ 6.15 ± 0.28, 11 ♀♀	10.74 ± 0.62, 21 ♂♂ 10.54 ± 0.67, 11 ♀♀	13.10 ± 0.14 (2)
Zonotrichia capensis	8.98 ± 0.41, 11 ♂♂ 8.65 ± 0.24, 4 ♀♀	7.88 ± 0.35, 11 ♂♂ 7.70 ± 0.46, 4 ♀♀	—
Vireo olivaceus	9.97 ± 0.66, 11 ♂♂ 9.22 ± 0.10, 3 ♀♀	9.17 ± 0.79, 11 ♂♂ 9.38 ± 0.15, 4 ♀♀	14.6 (1)
Elaenia parvirostris	6.36 ± 0.19, 6 ♂♂ 6.15 ± 0.07, 2 ♀♀	8.23 ± 0.75, 6 ♂♂ 9.35 ± 0.92, 2 ♀♀	—
Elaenia albiceps	6.76 ± 0.14, 3 ♂♂ 7.38, 1 ♀	8.85 ± 0.64, 2 ♂♂ 9.00, 1 ♀	—
	Type II		
Tachyphonus coronatus	11.15 ± 0.77, 20 ♂♂ 11.22 ± 0.39, 10 ♀♀	10.18 ± 0.72, 20 ♂♂ 9.95 ± 0.68, 10 ♀♀	12.10 ± 0.74 (7)
Trichothraupis melanops	9.20 ± 0.45, 18 ♂♂ 9.76 ± 0.33, 11 ♀♀	9.76 ± 0.68, 18 ♂♂ 10.04 ± 0.79, 11 ♀♀	14.02 ± 1.64 (16)
	Type III		
Tangara seledon	7.49 ± 0.37, 5 ♂♂ 7.76 ± 0.13, 2 ♀♀	7.58 ± 0.57, 4 ♂♂ 8.15 ± 0.21, 2 ♀♀	—
Dacnis cayana	9.38 ± 0.47, 7 ♂♂ 9.74 ± 0.23, 4 ♀♀	6.81 ± 0.50, 7 ♂♂ 6.91 ± 0.17, 4 ♀♀	12.30 ± 0.71 (2)
Coryphospingus cucullatus	8.36 ± 0.32, 13 ♂♂ 8.18 ± 0.44, 6 ♀♀	7.62 ± 0.44, 15 ♂♂ 7.70 ± 0.34, 6 ♀♀	—
Euphonia violacea	6.10 ± 0.14, 2 ♂♂ 6.42 ± 0.16, 3 ♀♀	7.75 ± 0.50, 2 ♂♂ 7.50 ± 0.72, 3 ♀♀	8.23 ± 1.97 (3)
Chlorophonia cyanea	6.52 ± 0.26, 2 ♂♂ 6.03, 1 ♀	7.60 ± 0.28, 2 ♂♂ 7.30, 1 ♀	6.50 ± 1.41 (2)
Euphonia pectoralis	6.43 ± 0.12, 3 ♂♂ 6.60, 1 ♀	7.67 ± 0.60, 3 ♂♂ 7.1, 1 ♀	10.0 (1)
Hemithraupis guira	8.70 ± 0.67, 7 ♂♂ 9.21 ± 0.55, 4 ♀♀	7.71 ± 0.42, 7 ♂♂ 8.43 ± 0.12, 3 ♀♀	12.8 (1)
Euphonia chlorotica	5.71 ± 0.39, 4 ♂♂ 5.95 ± 0.78, 2 ♀♀	6.90 ± 0.61, 3 ♂♂ 6.20, 1 ♀	6.3 (1)

[1] *Mionectes rufiventris*, feeding type undetermined, bill length = 8.72 ± 0.27 mm, 6 ♂♂; 8.72 ± 0.06 mm, 2 ♀♀; rictal width = 8.15 ± 0.54 mm, 6 ♂♂; 7.95 ± 0.35 mm, 2 ♀♀.

TABLE 5. Estimated number of fruits and feeding times needed by selected bird species to meet daily energy requirements for existence (DEE), social maintenance (DSE), and reproduction (DRE) when consuming only *A. edulis.*

Species	DEE (DSE/DRE): kcal[1]	No. fruits[2]	Total time min[3]	Time min/g body wt.[4]
		Type I		
Turdus rufiventris	26 (44/70)	128 (213/342)	2 (4/6)	0.03 (0.06/0.08)
Turdus leucomelas	25 (42/67)	123 (206/329)	3 (4/6)	0.04 (0.06/0.09)
Chiroxiphia caudata	12 (21/33)	60 (101/161)	3 (5/7)	0.13 (0.22/0.30)
		Type II		
Tachyphonus coronatus	13 (22/35)	83 (139/222)	33 (55/87)	1.22 (2.04/3.22)
Tachyphonus melanops	11 (19/30)	97 (162/259)	27 (44/70)	1.23 (2.00/3.18)
		Type III		
Euphonia chlorotica	8 (14/22)	68 (114/182)	36 (60/95)	2.77 (4.62/7.31)
Euphonia violacea	9 (16/25)	78 (131/209)	42 (69/110)	2.80 (4.60/7.33)
Euphonia pectoralis	8 (14/22)	72 (121/193)	51 (85/136)	3.64 (6.07/9.71)
Hemithraupis guira	8 (14/22)	108 (181/289)	51 (85/135)	3.64 (6.07/9.64)

[1] Calculated for the greatest weight given for the species in Table 2; values rounded to the next higher kcal.
[2] Calculated by dividing DEE by the product of the energy content of an average fruit, the mean percent of pulp eaten per fruit (from Table 3), and the assimilation efficiency; or, no. fruits = DEE ÷ (0.23 × $\bar{x}$ % pulp eaten/fruit × 0.9). Values rounded to the next higher whole number.
[3] Calculated as no. of fruits (from column 3) × $\bar{x}$ handling time/fruit (from Table 3) ÷ 60. Values rounded to the next higher minute.
[4] Total time (from column 4) ÷ the greatest weight for the species in Table 2.

meet its DDE needs when feeding on *Allophyllus,* while *T. melanops,* a Type II feeder, would require 1.23 min. *Euphonia chlorotica,* a Type III feeder which weighs only slightly more than half that of the former two species, requires 2.77 min feeding time/g body weight.

DISCUSSION

SIZE, BILL DIMENSIONS, AND FRUIT HANDLING

Feeding methods for birds using *A. edulis* were very similar to those reported for 26 species of birds feeding on the arillate fruits of *Bursera simaruba* in Panama (Trainer and Will 1984). As shown in that study, handling method and body size (weight) are not necessarily correlated. Birds feeding with Type II and III methods tend to be small, but species of all sizes are represented among those feeding with Type I methods. It is more likely that foraging method is correlated with some aspect of bill morphology. Although bill dimensions do reflect body size, increases in each are not necessarily proportional. In particular, small birds may have bills proportionally larger than those of their larger counterparts (Table 4). Thus, large birds generally have bills that are large relative to size of the fruit, while small birds may have bills large or small relative to fruit size.

The way in which any given fruit is handled probably is a facultative response determined by the size of fruit relative to the size of the bill. One can hypothesize the existence of a size threshold for each bill dimension below which a bird is unable to feed in a particular way. Wheelwright (1985), for example, demonstrated that the size of fruit that can be swallowed is correlated with width of the bill at the rictal commissure. Rictal widths of most Type III feeders appear to fall below such a limit for *Allophyllus,* preventing these birds from swallowing the fruits whole. (*Euphonia* species routinely swallow the smaller, whole fruits of various species of mistletoes and epiphytic cacti [pers. observ.].) There is, however, no clean cutoff point. The rictal width of *Zonotrichia capensis,* a Type I feeder, overlaps those of three Type III species, and four species that swallowed fruits whole had mean rictal widths less than those of both Type II species (Table 4).

Another important dimension that may confound the correlations between gape width and fruit diameter is tip gape. Before a bird can swallow a fruit whole or cut the pulp from the seed, it must be able to open its bill wide enough to grasp and manipulate the fruit. And, if a bird does this, then by mashing or cutting some pulp from the seed, it may be able to reduce the overall diameter of the fruit to a point below the threshold for swallowing it whole. Tip gape is a function of both the length of the mandibles, and the degree to which they can be rotated open at the base, factors that appear to be independent. For example, five species (Table 4) with mean bill lengths of 5.71 to 6.60 mm had tip gapes of 6.3 to 13.1 mm, while six species with tip gapes of 12.1 to 14.6 mm had bill lengths of 6.15 to 11.22 mm. In fact, tip gape as a proportion of bill length and bill length were significantly correlated (r_s = 0.3516, Spearman's Rank; Student's t = 1.245; $P > 0.10$, df = 11). Both bill lengths and tip gapes overlapped considerably among the birds in the three feeding categories. Several Type III species with bills that appeared too small to grasp or manipulate an *A. edulis* fruit did so occasionally, but clumsily (e.g., *E. violacea* and *C. cyanea*; see Appendix).

Even if minimum bill dimension thresholds exist, possession of a bill with measurements greater than threshold does not necessarily indicate that a bird will handle a food item in a particular way (cf., Carothers 1982). This was true for the birds feeding on *Bursera simaruba* (Trainer and Will 1984) as well as for those eating *Allophyllus. Thraupis sayaca,* for example, used all three handling methods. Both species of Type II feeders have bills large enough to allow them to grasp fruits and swallow them whole but were observed to do this on only very few occasions (see Appendix). Bill dimensions of *Vireo olivaceus, Dacnis cayana,* and *Hemithraupis guira* approach those of the Type II feeders, yet the former species was only observed to swallow fruits whole, and the latter two, although they occasionally mashed fruits, were not observed to cut the pulp from the seed.

Two conclusions that may be drawn from the above discussion are (1) that bill dimensions do not always predict the way in which a bird will handle a fruit, and (2) that birds do not necessarily handle particular fruits in the most efficient way available to them. This is clearly illustrated by *Thraupis sayaca, Trichothraupis melanops,* and *Tachyphonus coronatus.* It may be that esophageal and gastric morphology are of overriding importance, for example through their influence on passage or regurgitation of seeds. Likewise, manipulations such as those exhibited by Type II feeders may require sophisticated nervous control. Diamond et al. (1977) have also suggested that bill and palate strength, relative to fruit hardness, will influence the method of fruit consumption. Trainer and Will (1984), on the other hand, suggested that feeding methods used on a particular fruit species may reflect nothing more than the way in which a bird species handles food in general (though even this presumably is not serendipitous). However, handling techniques used by closely related bird species feeding on fruits of different form are not always similar (cf. McDiarmid et al. 1977).

FEEDING EFFICIENCY

Consideration of the impact of feeding efficiency on the bird species is important, given that some seem relatively inefficient. For all species, the number of fruits needed to meet daily existence energy requirements is small, and feeding time, rather insignificant (Table 5). This is especially striking given the relatively low energy content of individual *Allophyllus* fruits (e.g., McDiarmid et al. 1977, Foster 1978, Foster and McDiarmid 1983). The small number of fruits and short feeding times for the Type I species reflect their brief handling times and efficient pulp removal. Effective feeding time might be longer if presence of seeds in the digestive tract were to interfere with subsequent feeding. There is some evidence of this in birds that feed on fruits with large seeds (Moermond and Denslow 1985; N. T. Wheelwright, in litt.), but it was not apparent for Type I feeders on *Allophyllus. Turdus rufiventris* in cages ate as many as 8, 10, or 11 fruits in several bouts during periods 4, 15, and 20 min long, respectively, with seed regurgitation beginning ca. 12 min after the first fruit was eaten. Even the Type II and Type III species should be able to meet existence energy requirements in 30 to 60 min. When energy requirements for social maintenance and reproduction are considered, the number of fruits and feeding times are still quite small (Table 5), with 2.25 hr of feeding estimated to be sufficient for the least efficient species to meet its energy needs. It may be, of course, that needs for a particular mineral or nutrient (e.g., protein) are more constraining in terms of time. Certainly, protein content per fruit of *Allophyllus* is minimal and does not seem adequate to support growth of young (Foster 1978).

Although the feeding time values are estimates, they provide insight into the extremely short foraging times suggested for many frugivorous birds (Snow 1962a, b; Foster 1977) as well as the observation that many tropical birds with significant amounts of fruit in their diets appear to spend much of their time "loafing." Bird species whose diets include large quantities of fruit seem to be "time minimizers" (Schoener 1971). Some accomplish this by curtailing food handling time. Some, particularly those that specialize on plant species with regular fruiting schedules and massive crops, appear to know the locations of the trees and to spend little time searching for food except, perhaps, in times of severe food shortage. Frugivores should spend no time in pursuit of "prey," unless one includes flight time between feeding trees, or, perhaps, in testing and rejecting unripe or other "unsuitable" fruits. Others, such as Type III feeders may be both time minimizers and "energy maximizers" (Schoener 1971). Rather than attempting to remove all pulp attached to a seed, they exploit the easily removed fraction with a few bites and move to another fruit.

Although overall time spent feeding is small for all the birds considered here, some species are clearly less efficient than others at feeding on *Allophyllus* fruits and must spend significantly more time at it. This may not be important if these fruits are sufficiently abundant to preclude competition among the users, as was suggested by Willis (1966) for birds feeding on melastome fruits (but see Terborgh and Diamond 1970). Three observations suggest this: (1) interspecific and intraspecific aggressive interactions among individuals feeding in this tree species were rare; (2) no birds of any species were seen to visit certain trees with ripe fruit (Foster, unpubl. data); and (3) much of the fruit crop rotted or dried on the tree and fell to the ground before being eaten in several years during which fruits were monitored. In this case, interspecific differences in handling efficiency, at least relative to competition for food, may be irrelevant.

The significance of differences in feeding efficiency thus becomes a question of time and, perhaps, predation risk, i.e., if the birds were not feeding, what might they be doing instead, and could they be doing it in a safer place (Morse 1980)? Birds that are not feeding could at least by their presence maintain vigilance at a territory, attract or guard a mate, or defend young. Most of the species are breeding when *Allophyllus* is in fruit, and many are feeding young. More efficient feeders should have more time to search for insects to feed to nestlings, although nestling diets of many species may be supplemented with *Allophyllus* fruit. One may also speculate that if the birds spent less time feeding, they would not engage in as many inter- and intraspecific aggressive interactions. Such encounters most frequently involved Type III feeders, as would be expected given the significantly greater time these birds spend in *Allophyllus* trees, but overall, they were extremely rare anyway.

Information concerning predation pressure experienced by the birds is not available. Those that spend very little time feeding might have more flexibility in scheduling feeding bouts so as to minimize predation. Nevertheless, it seems unlikely that differential predation is correlated with feeding method. Four Type I species feed at least part of the time on the exposed outer surface of the crown (Appendix), but they spend relatively little time in the tree. Visits by Type II feeders are somewhat longer, and those of Type III species, considerably longer than those of Type I, but all but one species of the former two groups feed only in the undercrown of the tree. Thus, the birds should be protected from predation by aerially hunting predators, presumably their greatest risk. Despite the possible alternative activities and potential agonistic encounters, it appears that increases in handling time have a relatively trivial effect on the time/energy budget of these bird species, a finding in keeping with those of Leighton (1982) for hornbills.

SPECIALISTS AND GENERALISTS

Another observation that deserves comment is that primarily frugivorous birds are among the least efficient at handling *Allophyllus*. Implicit in trophic designations of organisms (e.g., as insectivores, frugivores) are the assumptions not only that the organisms consume primarily the food in question, but also that they are adapted to do so. Likewise, it generally has been accepted that the diversity of food items in the diet and the efficiency with which an organism uses each of them are inversely related (MacArthur 1972, Morse 1980). If true, then one can hypothesize that generalists should be less efficient than specialists at exploiting particular food items. For both these reasons, one would expect frugivores to be more efficient at feeding on fruit than birds that eat fruit and insects, and those to be more efficient than the omnivores.

The results presented here appear to counter this prediction. The first assumptions, although in general correct, are at best imprecise. Adaptations may exist at several levels, and a "specialist" does not necessarily exhibit all of them. Particularly important may be the efficiency with which birds of the various species digest and assimilate nutrients in the fruits. Obligate frugivores could be more efficient in these ways than are their omnivorous or largely insectivorous counterparts, which would compensate for their inefficiency in handling fruit (Moermond and Denslow 1985; but see Walsberg 1975 for an opposing view). As to the degree of diet specialization, most likely my results reflect the limited nature of the comparison, which involves only a single species of fruit rather than the entire range of food items used. "Specialization" is a relative term requiring a point or frame of reference. The species, as compared here, are more or less efficient relative to one another, *only* when feeding on *Allophyllus edulis.* Likewise the level at which the designations of generalist and specialist were made here is broad. A species that specializes on one class of foods (e.g., fruit) could exploit more kinds (i.e., species or morphotypes) of that food than a species that uses several classes of foods. Categories defined along other lines (e.g., range of food sizes or shapes exploited) might yield quite different results.

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APPENDIX

WEIGHTS, FEEDING HABITS, AND DIETS OF SPECIES OF BIRDS FEEDING ON *ALLOPHYLLUS EDULIS*

Weights given in parentheses as means ±1 SD. Stomach content data taken from Tirol birds collected in all months.

Elaenia albiceps. (3 ♂♂ = 16.4 ± 0.90 g; 1 ♀ = 15.0 g.) Single individual observed feeding in the crown of a Cocú tree; in the tree for 40 sec during which time it reached for, plucked, and swallowed two fruits whole. Three stomachs examined contained only fruit. Vigil (1973) indicated that the species feeds primarily on insects although it also takes fruit and buds.

Elaenia parvirostris. (7 ♂♂ = 16.5 ± 1.09 g; 3 ♀♀ = 18.3 ± 4.25 g.) Feeds in undersurface of the crown in upper half to third of the tree, by perching and plucking, hover-plucking, or grabbing a fruit on the wing. Typically takes two to four fruits per bout, often changing perches between fruits. Once the fruit is in the bill, the bird releases it very briefly and grabs it again further down the bill, rapidly swallowing it whole. Five specimens from Tirol had fruit or fruit remains in their stomachs; two had insect remains. Belton (1985) reported that the species was more frequently observed feeding on small fruits than on insects.

Elaenia spp. Two other species of *Elaenia* are common at Tirol. Observations of unidentified members of the genus may be of one of these (*E. flavogaster* [6 ♂♂ = 24.2 ± 2.85 g; 3 ♀♀ = 22.3 ± 0.68 g], *E. spectabilis* [3 ♂♂ = 28.4 ± 0.58 g; 1 ♀ = 25.5 g]) or of one of the above two species. Stomachs of three *E. spectabilis* and seven *E. flavogaster* contained only fruit. *E. flavogaster* reported to eat both fruits and insects (Haverschmidt 1968, Wetmore et al. 1984).

Mionectes rufiventris. (7 ♂♂ = 14.1 ± 1.06 g; 2 ♀♀ = 11.6 ± 0.57 g.) Only one observation of this species feeding in Cocú. I was unable to determine how the bird ate the fruit it plucked. Three stomachs contained fruit (including seeds), and one contained insects.

Pitangus sulphuratus. (8 ♂♂ = 62.75 ± 4.98; 6 ♀♀ = 66.3 + 6.40 g.) Feeds in outer surface of upper third of tree. Feeding bouts generally <1 min during which time bird may take as many as 10 fruits. Birds perch or hover, and reach out and pluck fruits, taking one to several at one time. Fruits swallowed whole. Stomachs of three birds contained only insects, five only fruits, two seeds and insects, and one, only seeds (probably indicative of fruit eating). Omnivorous diet (Haverschmidt 1968, Wetmore 1972, Vigil 1973) includes a wide variety of fruits (Voss and Sander 1980, 1981).

Myiodynastes maculatus. (9 ♂♂ = 43.8 ± 3.95; 2 ♀♀ = 50.75 ± 8.84 g.) Flycatches fruit from outer surface of upper parts of tree, or occasionally from underside of crown. Swallows fruits whole, usually one per bout. Four stomachs contained only insects, five only fruits, and two fruit and insect remains. Feeds on a variety of insects and fruits (Haverschmidt 1968, Voss and Sander 1980, Robbins et al., 1985, Wetmore 1972) and may also take small lizards (Wetmore 1972).

Empidonomus varius. (11 ♂♂ = 27.2 ± 2.90 g; 1 ♀ = 26.5 g.) Generally feeds in the top third of tree by reaching and plucking within the foliage, or flycatching fruit from the outer surface of the crown. One fruit taken per feeding bout, swallowed whole. Three stomachs contained only insects, five only fruit, and three, fruit and insects. Literature reports insects (Mitchell 1957), fruits (Voss and Sander 1980), and insects and berries (Haverschmidt 1968) in the diet.

Chiroxiphia caudata. (21 ♂♂ = 22.6 ± 1.15 g; 11 ♀♀ = 22.65 ± 1.61 g.) Feeds anywhere within the tree, perching and plucking fruits, hovering and plucking them, or snatching one on the wing. Fruits taken singly and swallowed whole after being rolled or "juggled" down the bill. Seeds regurgitated or passed in the feces. Although reported to feed on fruit and insects (Voss and Sander 1981, Vigil 1973), the species is primarily frugivorous (Foster 1985).

Pyroderus scutatus. (1 ♂ = 375 g; 1 ♀ = 330 g.) One female noted feeding within crown in upper part of the tree. She had one whole fruit of *A. edulis* in her esophagus, six whole fruits and 13 seeds in her stomach, along with one small insect and three seeds of *Cupania vernalis* Camb. (Sapindaceae), and 34 *A. edulis* seeds and four of *C. vernalis* in her intestine. Snow (1982) reported the species feeding on fruits and large insects (also one record of a bird); Vigil (1973) indicated a fruit diet.

Cyanocorax chrysops. (2 ♂♂ = 157.0 ± 11.31 g; 8 ♀♀ = 159.0 ± 7.33 g.) Generally feeds in interior of tree and grabs several fruits at one time. Two stomachs examined contained only insects; two contained seeds and insects; one was filled with fruit; one had insects, seeds, and rocks, and one grit, seeds, and other plant material. Omnivorous; feeds on invertebrates, vertebrates, fruits (Vigil 1973), and nuts (Voss and Sander 1980).

Turdus rufiventris. (13 ♂♂ = 66.8 ± 5.68 g; 10 ♀♀ = 72.2 ± 5.01 g.) Generally feeds in dense vegetation on inside of upper two-thirds of tree. Feeding bouts are short (<1 min), with the bird feeding in a small area of ca. 0.35 to 0.5 m^2. Reaches and plucks fruits swallowing them rapidly. Eats one to six fruits per bout at a rate of one fruit every 5 to 20 sec, with longer pauses between bouts. Swallows fruits by alternatively "letting go" of the fruit and grabbing it again, further into the bill. Cocú seeds regurgitated or passed in the feces. Nine stomachs examined contained only fruit, four only insects, and four both fruit and insects. Feeding on fruit noted commonly (Belton 1985; Voss and Sander 1980, 1981); also forages in lawns and gardens (Belton 1985), presumably for invertebrates.

Turdus leucomelas. (10 ♂♂ = 69.8 ± 4.73 g; 7 ♀♀ = 66.8 ± 6.76 g.) Feeds in inner surface of tree crown, high up toward center of the tree. Feeding bouts short (≤5 sec), during which a bird may consume as many as four fruits, by reaching and grabbing. Fruits are manipulated with the tongue and swallowed whole. Birds eat several fruits in rapid succession, pause for 30 to 60 sec, and then feed again. Seeds regurgitated at intervals of 2 min or less. There is a visible pulsing of the throat, followed by a pause of 30 to 60 sec, another pulsing of the throat, and the seed is thrown out the tip of the bill. Stomachs of eight birds contained fruit; one stomach contained seeds and insects. Generally consumes fruits and insects (Vigil 1973, Belton 1985), though small lizards may also be taken (Haverschmidt 1968).

Turdus amaurochalinus. (5 ♂♂ = 63.1 ± 6.30 g; 3 ♀♀ = 63.0 ± 8.89 g.) Feeds in dense vegetation in upper portions of tree. Usually changes perches between feedings. Reaches and plucks fruits, swallowing them whole. Birds generally stay in tree for <1 min. One stomach contained fruit, one fruit and insects. Diet reported to include fruit, flowers, and insects (Vigil 1973; Voss and Sander 1980, 1981; Belton 1985).

Vireo olivaceus. (20 ♂♂ = 15.25 ± 0.86 g; 8 ♀♀ = 14.9 ± 1.31 g.) Feeds in inner core of upper part of tree by reaching (often with acrobatic poses) and plucking fruits while perched or hovering. After swallowing, the bird jerks its head back and forth, as if moving the fruit down its esophagus. Regurgitates completely cleaned seeds. Fifteen stomachs examined contained only insects, five contained only fruit, and two both fruit and insect material. Both fruit and insect eating reported previously (Haverschmidt 1968, Vigil 1973).

Zonotrichia capensis. (22 ♂♂ = 20.1 ± 4.25 g; 4 ♀♀ = 20.3 ± 2.17 g.) Two birds observed eating Cocú on one occasion. One ate three fruits, the other two. They reached, plucked, and swallowed the fruits whole. Species known to eat both insects and seeds (Vigil 1973, Belton 1985); also reported to take fruit (Voss and Sander 1980, 1981). Whether seeds are consumed or dispersed is not clear. Seven stomachs from Tirol contained only seeds, 12 only insect remains, and three remains of both insects and seeds.

Coryphospingus cucullatus. (20 ♂♂ = 14.9 ± 1.25 g; 12 ♀♀ = 14.85 ± 1.95 g.) Feeds in outer shell of vegetation in upper part of tree by reaching and plucking fruits. Birds take small bites of pulp from a fruit held on a perch with the foot, and drop cleaned seed. May eat one to five fruits per bout. Insects or insect remains found in 10 stomachs, plant material, seeds, or seed fragments in four. Reported to eat fruit (Voss and Sander 1980), insects, and seeds (Vigil 1973).

Hemithraupis guira. (11 ♂♂ = 12.8 ± 0.70 g; 6 ♀♀ = 13.9 ± 0.95 g.) Consistently feeds in the top outer surface of trees. Birds take fruits by reaching and plucking or by plucking as they fly by; frequently take bites of fruits that remain attached to the tree. Sometimes mashes fruits in its bill with big wads of pulp piling on top. More often manipulates fruit against a horizontal perch; appears to stab pulp with upper mandible and roll fruit with tongue and lower mandible, cutting off pulp. Eight birds had only insect remains in their stomachs, three had only fruit, and three had both insect and fruit remains. Reported to eat both fruit and insects (Haverschmidt 1968, Voss and Sander 1980), or primarily insects (Isler and Isler 1987).

Tachyphonus coronatus. (24 ♂♂ = 26.2 ± 2.85 g; 13 ♀♀ = 26.7 ± 2.58 g.) Generally feeds in upper third of tree on undersurface of the crown or in it. Reaches and plucks fruits and frequently moves between perches and calls while feeding. One to three fruits taken per bout. Most commonly (143 of 146 observations) these are eaten with Type II methods. Three times a bird swallowed a fruit whole and regurgitated the cleaned seed. Eleven stomachs examined contained only insects, five only fruit, and six combined remains of fruit and insects. Species reported to eat fruit and flowers (Voss and Sander 1980, 1981; Belton 1985).

Trichothraupis melanops. (25 ♂♂ = 20.4 ± 1.75 g; 15 ♀♀ = 21.8 ± 1.32 g.) Feeds primarily in upper third of tree in crown vegetation. Occasionally grabs a fruit while perched, or hovers and plucks one, but most commonly makes "flycatching sallies" grabbing a fruit on the wing while flying between perches. Usually eats one to four fruits per feeding bout, but spends time changing perches, examining different fruits, and calling. Only six of 250 fruits eaten were swallowed whole; the rest were eaten with Type II methods. Only insects were found in 21 stomachs examined, only fruit in six, and both fruit and insect remains in two. The stomach of a bird examined by Belton (1985) contained insect remains.

Thraupis sayaca. (6 ♂♂ = 31.25 ± 1.13 g; 9 ♀♀ = 33.5 ± 1.45 g.) Generally feeds in thick foliage at crown of tree. Showed the most varied feeding patterns of any species in Cocú, handling fruit with Type I, II, and III methods. Feeding episodes involving 44 fruits were observed in their entirety. Twenty-six of the fruits were swallowed whole, 13 were rolled in the bill, the separated pulp swallowed and the seed dropped, and five were held against a branch while bites of the pulp were removed. Birds fed by perching, reaching, and plucking, and sometimes carried fruits from the tree before swallowing them. One bird took eight fruits in a bout, but the usual number was two to three. Four stomachs examined contained only fruit or seeds, one only insects, and two insects and flowers or plant material. Insects, fruit, buds, and shoots reported in the diet (Mitchell 1957; Haverschmidt 1968; Voss and Sander 1980, 1981; Belton 1985; Isler and Isler 1987). Although this species is reported to flycatch for insects (Haverschmidt 1968, Belton 1985), I did not observe these tanagers taking fruit in this manner.

Euphonia chlorotica. (3 ♂♂ = 11.6 ± 1.21 g; 2 ♀♀ = 13.0 ± 1.41 g.) Observed only in undersurface of "bowl" of crown, high up toward center. Most commonly feeds by taking small bites of fruits that remain attached to tree. Occasionally plucks a fruit and removes pulp by pushing fruit against a horizontal branch. Birds are very selective, examining many fruits before feeding. Usually take only a few bites from a fruit before moving to the next. Stomachs of two birds contained only fruit, which is their reported diet (Voss and Sander 1980, 1981; Belton 1985; Isler and Isler 1987).

Euphonia violacea. (4 ♂♂ = 14.1 ± 0.66 g; 2 ♀♀ = 14.5 ± 0.71 g.) Stays on underside of crown in upper third of tree. Moves frequently and examines fruits carefully before selecting one. Often assumes acrobatic postures when feeding. When a fruit is plucked, the bill usually penetrates the pulp giving the impression that the bird has stabbed the fruit. May take bites from the fruit as it rests on the perch or roll it against the branch. Sometimes also rolls it in the bill cutting the pulp, with wads piling up on top of the bill. Family groups, including recently fledged young, observed feeding in *Allophyllus* trees. Stomachs of two birds examined contained pulp of *A. edulis.* Reported to feed on fruit (Haverschmidt 1968, Isler and Isler 1987).

Euphonia pectoralis. (4 ♂♂ = 13.8 ± 0.83 g; 1 ♀ = 13.8 g.) Observed feeding on Cocú on only two occasions. One bird ate two fruits, another five. A third individual observed feeding in a cage ate 14 fruits. In every instance they were plucked and carried to a horizontal branch, and the pulp removed. One Tirol bird had fruit remains in its stomach. Reported to feed on fruit (Voss and Sander 1981).

Chlorophonia cyanea. (2 ♂♂ = 13.75 ± 0.35 g; 2 ♀♀ = 15.25 ± 1.06 g.) Feeds on underside of canopy in upper third of tree. Frequently changes perches in tree, and examines fruits carefully before selecting one. Feeding bouts long; birds often stay in tree up to 20 min. May take bites from fruits that remain attached to the tree, often moving from a fruit after consuming very little of it. Occasionally plucks a fruit and mashes it in the bill before dropping the seed. Most commonly, however, fruit is carried to a horizontal branch; the bird, leaning over beyond the horizontal, pushes the fruit against the branch, rolling, and turning it in its bill and removing bits of pulp. Often perches erect, and mouths and swallows pulp between bites. Family groups observed feeding in *Allophyllus.* Stomachs of two Tirol birds contained fruit remains.

Tangara seledon. (6 ♂♂ = 18.5 ± 1.18 g; 2 ♀♀ = 20.5 ± 0 g.) Generally feeds in foliage in crown of upper third of tree, reaching and plucking one fruit at a time. Classified as Type III feeder because it usually pushes or rolls a fruit against a branch when removing pulp. Occasionally retains the fruit in the bill, opening and closing the bill against it, and mashing the pulp. Once a bird appeared to swallow a seed with the mashed pulp. Sometimes rolls the fruit in the bill, removing the pulp, but never cleanly cuts it in long strand as is characteristic of Type II feeders. Four stomachs examined contained fruit, and two "plant material." Reported to take some insects as well as fruit; records of seeds probably indicate fruit eating (Vigil 1973, Voss and Sander 1981).

Dacnis cayana. (7 ♂♂ = 15.9 ± 0.68 g; 5 ♀♀ = 16.1 ± 1.29 g.) Feeds only in the undersurface of canopy. Although capable of plucking fruits, often takes bites from fruits that remain attached to tree. One male fed from a cluster of four fruits randomly taking bites from them without completely eating any one. Extremely acrobatic when feeding, reaching and hanging, often upside-down. On one occasion (of 14) a male mashed a fruit in his bill for ca. 10 sec and then swallowed the seed. Stomachs of 11 specimens contained only fruit; one contained insects. Diet reported to include fruits and some insects; reports of visits to flower heads may signal nectar or insect feeding (Mitchell 1957, Haverschmidt 1968, Wetmore et al. 1984).

Cacicus haemorrhous. (7 ♂♂ = 101.9 ± 8.01 g; ♀♀, no weights.) Feeds in outer surface at top of tree. Usually perches, leans, and grabs fruits taking several at one time. Fruits swallowed whole almost immediately. Feeding bouts last ca. 15 sec. Stomach of one individual contained insects, of another, insect larvae; two had fruit. Reported to feed on fruits (Voss and Sander 1980, 1981) and berries (Mitchell 1957).