

Adaptations for avian frugivory: assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis*

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Summary. I examined the digestive physiology of two avian frugivores, the golden-collared manakin, *Manacus vitellinus*, and the red-capped manakin, *Pipra mentalis*, to discover how these birds extract energy from fruit. Using 14 species of fruit in the natural diet of manakins, I examined the assimilation of nutrients from fruit pulp, fruit passage rates, seed passage rates, and gut morphology. Fruits in the manakins' diets had high water content (average, 84%) and low nutrient concentrations (3 kJ/g wet pulp; 17 kJ/g dry pulp; 1% nitrogen/g dry pulp). *Manacus* and *Pipra* did not differ in the average assimilation of energy in fruit pulp (63%), although it varied from 37 to 84% depending on fruit species. Assimilation of total nonstructural carbohydrates in the fruit pulp was very high (86–98%) in both species. Gut evacuation was rapid; maximum transit time of a labeled fruit was 30 min. Seeds passed through the gut faster (*Manacus*: 15 min; *Pipra*: 12 min) than the accompanying fruit epidermis (both spp: 22 min). Manakins regurgitated large seeds (>5 mm diameter) in 7 to 9 min. Rapid gut passage time, high assimilation of nonstructural carbohydrates, and the selective regurgitation and rapid elimination of bulky seeds enable manakins to process a large volume of food per day. By increasing rates of fruit intake and gut passage, manakins can effectively increase total nutrient uptake. These adaptations of manakins are requisite for harvesting sufficient nutrients from fruit, due to its low nutrient density, high water content, and bulky seeds.

Key words: Avian ecology – Frugivory – Fruit-eating birds – Digestion – Gut transit time

Optimization processes evolve under certain constraints. A limiting factor in meeting daily food requirements can be the time taken to digest food. Digestion is known to be a rate-limiting step in the energy intake of herbivores (Sibley 1981) and nectarivorous hummingbirds (Diamond et al. 1986), and models of food choice now incorporate these constraints (Belovski 1978, 1984; Taghon 1981; Speakman 1988).

Digestion is likely to be an important constraint in the foraging ecology of frugivorous birds. Fruits are relatively poor in quality, with low nutrient density, high water con-

tent, and indigestible seeds (Snow 1970, 1981; Stiles 1980; Herrera 1981, 1982; Moermond and Denslow 1986). These properties require that avian frugivores either find and consume large quantities of fruit or select only high quality fruits. Frugivorous birds consume remarkably diverse diets. Emerald Toucanets (*Aulacorhynchus prasinus*) feed on 95 species of fruit (Wheelwright et al. 1984); manakins in Trinidad and Panama eat about 70 species of fruit (Snow 1962a, b; Worthington 1982, 1989); Costa Rican saltators include 189 fruit species in their diet (Jenkins 1969, cited by Moermond and Denslow 1986). However, frugivores are known to select among fruits based on high pulp to seed ratio (Howe and Vande Kerckhove 1981; Herrera 1981), seed size (Sorenson 1984), pulp mass (Johnson et al. 1985), sugar concentration (Levey 1987a), fruit size (Moermond and Denslow 1983), and ease of harvest (Moermond and Denslow 1983). Considering the seasonal phenology of fruit trees and the regularity of fruit shortages (M. Foster 1977; R. Foster 1982a, b; Worthington 1982, 1989), frugivores frequently cannot be selective. Therefore, to survive seasonal shortages or periods of reduced diversity of fruit, avian frugivores must be capable of processing large quantities of low quality fruits.

The energy content of a food does not necessarily reflect the value of that food to the animal. Digestive efficiency or assimilation (the proportion of the food or nutrient consumed that is actually digested and absorbed) is dependent on enzyme activity, density of transport proteins, gut size, gut transit time, and the nutrient content of the food (Robbins 1983). Several characteristics of a fruit can influence its digestion and assimilation. One such characteristic is water content; water-soluble nutrients are easily assimilated, and solutes move through the avian digestive tract faster than organic particles (Gasaway et al. 1975; Warner 1981). Another important characteristic is the amount of indigestible bulk, since large particle size (e.g. seeds or organic matter) and high fiber content can increase retention time of food (Sibley 1981; Warner 1981).

The two species used in this study, *Pipra mentalis*, the red-capped manakin (14 g), and *Manacus vitellinus*, the golden-collared manakin (18 g), are the most common understory frugivores in the lowland forests of Panama (Karr 1971; Worthington 1982). Fruits found in the manakins' diet typically have low concentrations of nutrients and high amounts of water and yet contribute 98% of the birds' dry matter intake (Worthington 1982, 1983, 1989). Caged manakins show definite fruit preferences (Moermond and

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Denslow 1983, Levey et al. 1984) but gut samples from free-living animals show high fruit diversity and a lack of selectivity (Worthington 1983).

I investigate here the digestive processes of *Pipra* and *Manacus* which explain how their digestive system processes dilute and bulky food. I examined energy and nutrient assimilation, morphological features, and gut transit time using 14 species of fruit found in the natural diet of manakins.

Methods

The experiments were carried out at the Smithsonian Tropical Research Institute's field station on Barro Colorado Island (BCI), Panama, during June through November, 1980. I netted wild manakins monthly from the low understory of primary and second growth lowland forest and held 8 *Manacus* (7 female, 1 male) and 6 *Pipra* (4 females, 2 males) for 3 to 19 days. The birds were housed individually in pyramid-shaped cloth cages, 45 × 45 × 90 cm, which enabled complete collection of feces. The caged birds were kept in a screened building with natural ambient temperature and light and were maintained on a mixture of wild fruits. At least 5 species of seasonally available wild fruits were collected daily and fed *ad libitum*. Birds maintained body mass and condition on this diet and appeared in good health throughout the study. Feeding trials began as soon as a bird's body mass stabilized in captivity.

For the feeding trials I used a variety of berries, drupes, and arils found in the natural diets of the birds. The 14 fruit species used in this study comprise 67% of the annual diet of wild manakins (Worthington 1982, 1989). Pulp samples from each fruit species were dried and stored for later analysis of energy, nitrogen, and total nonstructural carbohydrates (TNC). I measured energy content of fruit pulp and excreta on all samples in triplicate using a Parr microbomb calorimeter. The difference between triplicate subsamples was generally less than 1%. Samples of fruit pulp and excreta were analyzed by the University of Alaska Plant and Soil Lab for nitrogen (N) and total nonstructural carbohydrate (TNC) content. Plant TNC was determined using the modified Weinmann method which removes sugars, starches, and fructans. Total nitrogen content was determined by Kjeldahl digestion using a Technicon BD-20 apparatus. Because of a shortage of fecal material, N content was analyzed for only 7 fruit species fed to *Pipra* and 6 fruit species fed to *Manacus*. Sugar content was measured in the fruit juice of 6 species in the field using a Fisher high contrast hand refractometer. I scored fruits for the presence or absence of lipids; if a small sample of dry fruit left an oil stain on a piece of filter paper, the species was scored as "oily".

Assimilation efficiency. In order to understand what influences the amount of nutrients and energy available to manakins in fruit, I fed captive birds fruit species that varied in total size, and the content of seeds, water, and energy and measured the birds' assimilation efficiency. Assimilation efficiencies were computed as the ratio of energy (kJ) ingested minus the energy excreted to the energy ingested. For example,

$$\% \text{ energy assimilation} = 100 \times \frac{K_i - K_e}{K_i},$$

where K_i = energy ingested (kJ per g dry pulp × g dry pulp ingested) and K_e = energy excreted (kJ per g excreta × g dry excreta).

Beginning the afternoon before a feeding trial, birds were fed exclusively with the test species of fruit. In the evening all fruit was removed from the cage. At dawn, the bird was put into a clean cage with a known weight of fruit and allowed to feed. Water was also available *ad libitum*.

Duration of feeding trials was either 6 or 12 h depending on the amount of ripe fruit available. Droppings fell onto plastic sheets on the cage floor. I collected the sheets, weighed the remaining whole fruit, and removed all seeds from the feces. I included regurgitated fruits in the fecal sample since these fruits had been manipulated, squeezed, and partially digested by the stomach. To calculate the amount of pulp ingested, I subtracted the weight of seeds in the feces from the total weight of fruit eaten. The seedless feces were weighed fresh. The samples of fruit pulp and feces were dried at 60°C to a constant weight. I ground the dried samples in a Wiley mill using a 20 mesh screen and stored them in plastic bags for analysis.

Urinary tract excretions could not be separated from fecal excreta. I observed no white urate-like paste in feces of birds in these feeding trials, and the feces were visually indistinguishable from crushed fruit pulp.

For 14 of 23 trials I was only able to supply enough fruit to test one individual bird per species of fruit. To examine the magnitude of individual variation in assimilation efficiency I ran multiple trials at 2 to 3 day intervals using three *Manacus* fed *Coccoloba manzanillensis*. The number of trials per individual was 3, 2, and 2. A one way ANOVA was applied to arcsine transformed data (Sokal and Rohlf 1981). Within an individual the range of assimilation efficiency was small (74–81%, 80–82%, 81–82% for the three individuals tested). Variation among individuals accounted for 5.9% of the total variance and variation within individuals fed *Coccoloba* accounted for 94%. For interpreting experiments, I assumed that differences among individuals of a species are insignificant.

Gut passage. Following each assimilation experiment, I used the same bird to measure gut transit time, using three methods: marking fruit epidermis, accounting for seeds, and inserting colored beads into the fruit. Gut transit time was defined as the time from ingestion of a fruit to the first appearance of a marker in the feces (Warner 1981) and average transit time for a fruit component (fruit epidermis or seed) was calculated from mean transit times of that component in each fruit species. To study the passage of fruit epidermis, I marked fruits with a small spot of contrasting enamel paint. For fruits containing a single seed, seed passage was inferred by comparing the time and sequence of ingested fruit and voided seeds. For fruits containing more than one seed, I measured the time from first ingestion to the first evacuation of feces containing seed of that species. Small plastic beads (maximum diameter = 1.5 mm) were inserted into the fruit and their passage timed. In 9 fruit species, I timed the passage of at least two markers simultaneously. In 4 species, only seed passage was recorded. Each marker was measured 1–14 times per fruit species (mean = 6).

In each trial, a continuously observed bird was presented with a tray of 6 uniquely marked fruits. I recorded

Table 1. Characteristics of 14 species of fruit used in feeding experiments. Numbers in parentheses are the number of fruits dissected and weighed to calculate means of each parameter. Asterisk (*) indicates fruit which had oily pulp

Fruit species	Average per fruit:					
	Total wet mass (g)	Wet pulp (g)	H ₂ O in pulp (%)	Dry pulp (g)	Number of seeds	Total seed mass (g)
<i>Anthurium brownii</i>	0.1065 (25)	0.0745	79.4	0.015	2	0.0320
<i>Anthurium clavigerum</i>	0.0795 (31)	0.0647	79.7	0.013	2	0.0148
<i>Byrsonima crassifolia</i> *	0.9332 (11)	0.7989	73.1	0.215	1	0.1343
<i>Carludovica palmata</i>	0.6301 (10)	0.4800	84.5	0.074	> 50	0.1501
<i>Coccoloba manzanillensis</i> *	0.2107 (24)	0.1552	79.5	0.032	1	0.0563
<i>Doliocarpis dentata</i>	1.0474 (17)	0.7874	87.1	0.102	1	0.2600
<i>Doliocarpis major</i>	0.2149 (25)	0.1376	85.7	0.020	1	0.0773
<i>Guatteria amplifolia</i>	0.4693 (19)	0.3005	83.9	0.048	1	0.1688
<i>Hasseltia floribunda</i>	0.2275 (30)	0.1827	87.3	0.023	1–3	0.0448
<i>Heliconia latispatha</i> *	0.3351 (10)	0.1870	62.6	0.070	2–3	0.1481
<i>Palicourea elliptica</i>	0.1268 (25)	0.0839	90.2	0.007	2	0.0429
<i>Psychotria deflexa</i>	0.1171 (22)	0.1028	94.6	0.006	2	0.0114
<i>Psychotria horizontalis</i>	0.0821 (26)	0.0646	91.7	0.005	2	0.0175
<i>Psychotria marginata</i>	0.1638 (52)	0.1324	90.8	0.012	2	0.0315
Mean \pm SE	0.34 \pm 0.085	0.25 \pm 0.067	83.5 \pm 2.24	0.046 \pm 0.015		0.085 \pm 0.020

the time and color mark of each ingested fruit, regurgitated seed, and voided marker or seed. The time to regurgitate seeds in captivity did not differ from the time to regurgitate seeds in the wild (Worthington, unpubl. data). During the trials the birds had continuous access to either marked or unmarked fruits, thus avoiding unnatural gaps in gut filling. Average trial length (from first marker in to last marker out) was 45 min; thirteen fruit species were used in 30 trials. I recorded 1343 min of fruit feeding. During these continuous observations, I also recorded the temporal pattern of feeding and meal size. Each continuous record of feeding was analyzed to determine the interval between fruits eaten. From this analysis, a meal was defined as the number fruits eaten in a one minute period.

I obtained nine *Pipra* and seven *Manacus* from the field that died of accidental causes (e.g. mist-net accidents, flying into lab windows). Upon dissection, I removed the digestive tract and flushed it with water. I measured the length of the intestine from the pylorus to the cloaca. For 5 *Pipra* and 2 *Manacus* I measured body mass and empty gut mass.

Results

Fruit analysis

The three characteristics of fruit relevant to digestion are the high water content, low energy concentration, and the indigestible seeds. The fruits eaten by manakins were highly diverse in these three parameters (Table 1). For the 14 species of fruit, edible pulp had an average water content of 84%. As a result, concentration of energy was low in fresh fruit (3 kJ per gram wet pulp, SE=0.51). Mean energy content of dry fruit pulp was 17.33 kJ/g (Table 2). Dry fruit pulp contributed from 5% (in *Psychotria deflexa*) to 23% (in *Byrsonima crassifolia*) of the total fruit mass ingested (mean for all 14 fruit spp.=11.8%, S.E.=1.58). The proportion of wet fruit mass made up of edible pulp ranged from 58% in *Heliconia latispatha* to 87% in *Psychotria deflexa* (mean for all 14 fruit spp.=74%, SE=2.46). There-

fore, seed mass contributed from 13 to 42% of the mass ingested by the birds. The three species scored as "oily" (Table 1, see *) had significantly less water (72%) than "non-oily" fruit species (87%, Mann-Whitney U=34.4, $P<0.02$). Among these 14 fruit species, oily and non-oily fruits did not differ in energy content per unit dry mass. Percentage sugar in the pulp of 6 species averaged 7.8% (g/100 g solution, Table 2). Nitrogen content of fruit pulp averaged 1.06% of the dry pulp ($n=9$, S.E.=0.175, Table 4).

Energy assimilation efficiency

Pipra and *Manacus* did not differ significantly in overall mean energy assimilation for all fruit species tested (63%, Table 2, Wilcoxon's signed rank test $T_s=22.5$, n.s.). The cases of low assimilation (40% or less) were due to the inclusion of regurgitated fruits in the fecal sample. Only one bird from each species was tested on each of these fruits with low assimilation, and these individuals regurgitated whole fruits after the fruits had been manipulated and partially digested in the stomach. When these three fruit species were eliminated, the ranking of fruit based on energy assimilation efficiency was identical for the two bird species.

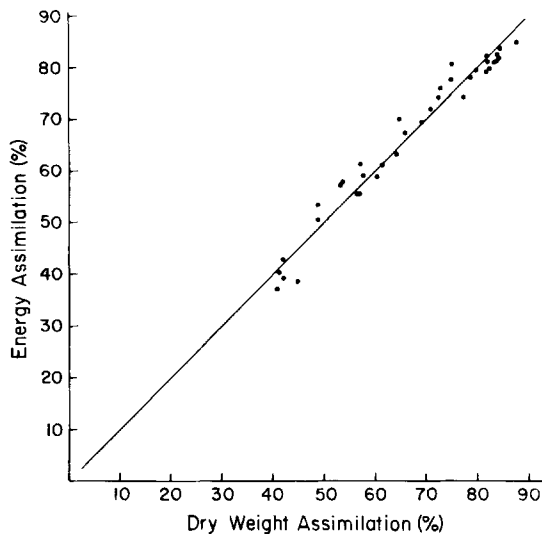
Assimilation of dry matter by mass accurately predicted the assimilation of energy as measured by bomb calorimetry (Fig. 1). This result confirms that all carbohydrate constituents of fruit (digestible starches, lignin, cellulose, sugars, etc.) have similar mass specific energy contents. Fruit species varied in the amount of assimilable constituents such as sugar (Table 2).

In *Pipra*, mass ingestion of dry pulp and mass production of feces were positively correlated (Spearman rank correlation, $r_s=0.586$, $n=15$, $P<0.05$). In *Manacus*, the trend was similar but not statistically significant ($r_s=0.338$, $n=20$, n.s.). For both species, as the energetic content of fruit pulp increased, energy content of feces also increased ($r_s=0.696$, $P<0.01$). In *Manacus*, fecal energy content was posi-

Table 2. Energy content, sugar content, and percent assimilation of energy in fruit pulp eaten by manakins. Fruit species are ranked according to energy content of fruit pulp

Fruit species	kJ per g dry pulp $\bar{X} \pm \text{SE}$ ($n = 3$)	% Sugar (g/100 g solution) $\bar{X} \pm \text{SE}$ ($n = \#$ fruit)	Assimilation of energy (%) $\bar{X} \pm \text{SE}$ ($n = \#$ of birds)	
			Pipra	Manacus
<i>Heliconia latispatha</i>	21.02 \pm 0.381		—	81 (1)
<i>Byrsonima crassifolia</i>	20.31 \pm 0.251		55 (1)	38 (1)
<i>Guatteria amplifolia</i>	18.55 \pm 0.197	12.0 \pm 1.21 (5)	40 (1)	58 \pm 5.0 (2)
<i>Palicourea elliptica</i>	18.38 \pm 0.243	6.8 \pm 0.33 (8)	53 (1)	57 (1)
<i>Hasseltia floribunda</i>	17.37 \pm 0.435		50 (1)	51 \pm 8.0 (2)
<i>Doliocarpus major</i>	16.83 \pm 0.142	12.8 \pm 0.30 (2)	78 (1)	79 (1)
<i>Doliocarpus dentata</i>	16.70 \pm 0.029		83 \pm 1.0 (2)	—
<i>Anthurium brownii</i>	16.45 \pm 0.230		47 (1)	49 \pm 10.0 (2)
<i>Coccoloba mazanillensis</i>	16.41 \pm 0.088		84 \pm 1.5 (2)	80 \pm 1.2 (6)
<i>Anthurium clavigerum</i>	16.37 \pm 0.439		76 \pm 1.8 (2)	37 (1)
<i>Psychotria marginata</i> ^a	16.24 \pm 0.109	5.3 \pm 0.11 (12)	65 \pm 4.0 (2)	70 \pm 2.5 (2)
<i>Psychotria horizontalis</i> ^a	15.49 \pm 0.134	4.3 \pm 0.08 (5)	61 (1)	58 (1)
<i>Psychotria deflexa</i> ^a	15.20 \pm 0.151	5.4 \pm 0.14 (5)	76 (1)	70 (1)
Means \pm SE	17.3 \pm 0.49	7.8 \pm 0.62 (6 spp)	64 \pm 4.4 (12 spp)	61 \pm 4.4 (12 spp)

^a 12-h feeding experiments, all others 6 h

**Fig. 1.** Relationship between dry mass assimilation of fruit pulp and energy assimilation of fruit pulp. Solid line represents a slope of 1 (F -test, $F_{1,35} = 892$, $P < 0.001$)

tively correlated with the amount of dry pulp ingested per feeding trial ($r_s = 0.497$, $P < 0.05$), but energy content of *Pipra* feces showed no trend with food intake ($r_s = 0.244$, n.s.). Correlations of the specific energy of fruit and feces and of fruit ingestion and the production of feces suggest that manakins have a fixed rate of absorption of energy no matter what the richness of the digesta. The more they ate, the more feces they produced, and the richer the food they ate, the richer the feces they produced.

There were no significant correlations ($P > 0.05$) of energy assimilation with water content ($n = 12$, $r = 0.109$), seed size ($n = 12$, $r = 0.305$), energy content ($n = 12$, $r = 0.476$), nitrogen content ($n = 8$, $r = 0.219$), or total nonstructural carbohydrate content ($n = 5$, $r = 0.398$).

Table 3. Assimilation [mean \pm SE (n)] of total non-structural carbohydrates (TNC). Fruit species are ranked according to TNC content

Fruit species	% TNC in dry pulp	% Assimilation of TNC	
		Pipra	Manacus
<i>Coccoloba manzanillensis</i>	53.3	97.5 \pm 0.50 (2)	97.6 \pm 0.15 (6)
<i>Anthurium clavigerum</i>	43.3	97.2 \pm 0.15 (2)	—
<i>Anthurium brownii</i>	43.3	86 (1)	—
<i>Doliocarpus major</i>	39.7	93 (1)	96 (1)
<i>Psychotria marginata</i>	38.8	88.5 \pm 1.5 (2)	95.5 \pm 0.50 (2)
<i>Carludovica palmata</i>	26.2	—	94 (1)
<i>Byrsonima crassifolia</i>	2.1	49 (1)	40 (1)

TNC assimilation

Assimilation of total nonstructural carbohydrates (TNC = sugars, starches) was very high (Table 3), *Pipra* had a mean TNC assimilation of 92.4% (SE = 2.30, $n = 5$ spp.); *Manacus* had a TNC assimilation of 95.8% (SD = 0.74, $n = 4$ spp.). Average TNC concentration for the 6 fruit species analyzed was 41% (S.D. = 8.78).

The TNC assimilation calculations above did not include *Byrsonima crassifolia*. *Byrsonima* had an unusually low TNC concentration (2.1%, Table 3); most of the carbohydrate energy in *Byrsonima* (20.31 kJ/g) must be structural. The TNC assimilation was also low, 49% for *Pipra* and 40% for *Manacus*.

Nitrogen balance

Short-term positive nitrogen balance for both bird species was achieved when nitrogen concentration in a fruit was greater than 1.3% (Table 4). The nitrogenous output included urinary contributions and therefore cannot be used to examine the digestibility of nitrogen in fruit. Since I fed the experimental animals with the test fruit species for only

Table 4. Nitrogen balance of *Pipra* (P) and *Manacus* (M) on a fruit diet. Fruits are ranked according to % N content in dry fruit pulp

Fruit species	% N (bird sp)	N intake (mgN/ day)	N output (mgN/ day)	Balance
<i>Palicourea elliptica</i>	2.14 (P)	49.0	49.0	-/+
<i>Heliconia latispatha</i>	1.36 (M)	39.8	29.3	+
<i>Anthurium clavigerum</i>	1.32 (P)	67.3	40.5	+
	(P)	66.9	42.7	+
<i>Psychotia deflexa</i>	1.30 (M)	18.5	17.6	+
<i>Hasseltia floribunda</i>	1.14 (M)	24.1	40.3	-
	(M)	31.3	38.2	-
<i>Psychotia marginata</i>	(P)	31.5	48.1	-
	1.00 ^a (P)	26.3	18.8	+
<i>Psychotria horizontalis</i>	(P)	29.5	26.3	+
	1.00 (M)	14.8	15.9	-
<i>Byrsonima crassifolia</i>	(P)	14.4	15.8	-
	0.82 ^b (M)	36.2	48.0	-
<i>Anthurium brownii</i>	0.42 (M)	7.0	14.6	-
Mean \pm S.E. (n)	1.06 \pm 0.175 (9 spp)			

^a SE = 0.028 (n = 2)

^b SE = 0.018 (n = 2)

Table 5. Digestive morphology of two manakin species and the mean transit time of seeds, fruit epidermis, and marker beads in their guts [mean \pm SE (n)]

	<i>Pipra mentalis</i>	<i>Manacus vitellinus</i>
Body mass (g)	14.2 \pm 0.12 (126)	female: 16.9 \pm 0.19 (78) male: 18.9 \pm 0.17 (57)
Intestine length (mm)	121 \pm 10.1 (10)	125 \pm 6.0 (7)
Empty gut mass/body mass	0.076 \pm 0.015 (5)	0.062 \pm 0.003 (2)
Gut transit time (min)		
Seed regurgitation	8.6 \pm 0.70 (8) ^a	6.8 \pm 0.98 (10)
Seed passage	11.5 \pm 1.43 (4)	15.1 \pm 2.24 (4)
Bead passage	11.9 \pm 2.11 (5)	14.6 \pm 1.32 (5)
Epidermis passage	22.3 \pm 2.51 (3)	20.5 \pm 1.75 (5)

^a n = # of fruit species, 1–14 measurements per species

the afternoon (6 h) preceeding the experiment, it is possible that the observed state of nitrogen balance was the result of longer-term effects of diet, activity or health prior to experimentation.

Gut evacuation

The time for interaction between ingested fruit and gut epidermis was short. The maximum transit time of a labeled fruit was 30 min. The fruit epidermis had the slowest rate of passage, averaging 21 min in *Manacus*, 22 min in *Pipra* (Table 5). Seeds passed through the gut more rapidly than fruit skin (15 min in *Manacus*, 12 min in *Pipra*, Table 5).

Why are gut transit times so fast? Manakins are small birds with no structure, e.g. crop, for storing food. The stomach is small, and no fruit is held in the distensible proventriculus (Fig. 2). Gut length of *Manacus* averaged

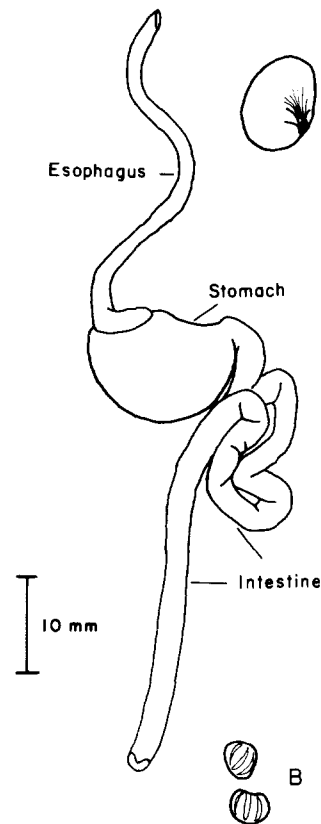


Fig. 2. The digestive anatomy of *Pipra mentalis*. To illustrate seed processing limits, A represents the largest seed swallowed and regurgitated (*Doliocarpus dentata*) and B represents the largest seed defecated (*Psychotria marginata*). Drawn from a photograph

125 mm and the gut length of *Pipra* averaged 121 mm (Table 5). The mass of the empty gut comprised about 7% of the body mass of manakins (Table 5). This is slightly smaller than the prediction of 9% for birds by Calder (1984).

Seed size had no influence on rate of passage of seeds through the gut. Seeds as large as 5 mm in maximum dimension and weighing 30 mg passed through the gut (Fig. 2). I inserted small beads (1.5 mm) in fruit to compare their passage with the passage of seeds through the gut. Beads and seeds passed through the gut of the manakins in 12 to 15 min (Table 5), with no difference between the two bird species or particle size.

Manakins regurgitated seeds larger than 5 mm maximum dimension (> 30 mg). The smaller species, *Pipra*, regurgitated seeds after 9 min on average and *Manacus* regurgitated seeds after 7 min (Table 5). Regurgitation of seeds was faster than defecation of seeds in *Manacus* (*t*-test, $P < 0.001$) but not in *Pipra* ($P > 0.05$). For seeds greater than 7 mm maximum dimension (> 50 mg) the birds did not take another fruit until the previous seed had been regurgitated. Besides seeds stripped of pulp, manakins could also regurgitate tough fruit skins, and whole fruits with the juice squeezed out.

Rate of passage of food was greatly influenced by the rate of food ingestion (Fig. 3). In *Pipra*, a high rate of food consumption decreased the transit time of a bead to as little as 7 min. However, as fruit consumption decreased, the transit time increased, plateauing at 15 to 20 min.

The laboratory observations of feeding demonstrated

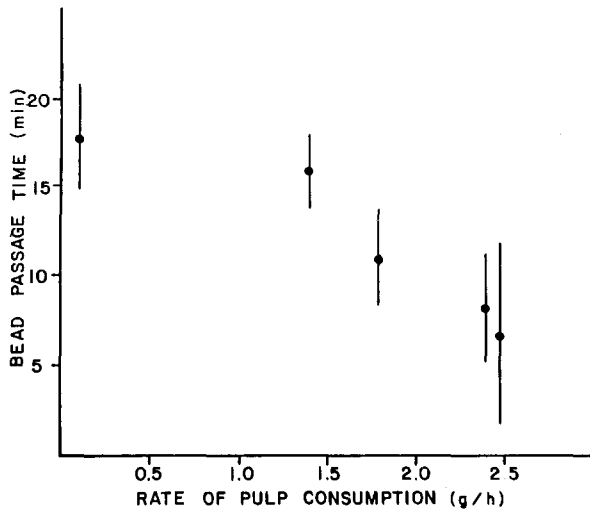


Fig. 3. Dependence of gut evacuation on the rate of fruit consumption in *Pipra*. Each point is the mean transit time of beads inserted into a particular species of fruit with an associated meal size. Vertical bars represent 95% confidence intervals

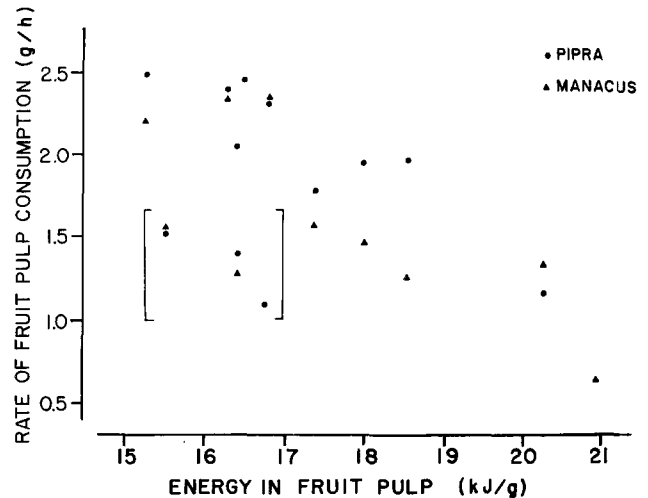


Fig. 5. Rate of fruit pulp consumption as a function of the energy in dry fruit pulp (F -test, $F_{1,20}=10.0$, $P<0.005$, $R^2=30.2\%$). Each triangle represents fruit fed *Manacus* and each circle represents fruits fed *Pipra*. Data within brackets represents meaningful departures from a highly predictive relationship ($R^2=79\%$ without data in brackets) due to gut capacity limitations (see text)

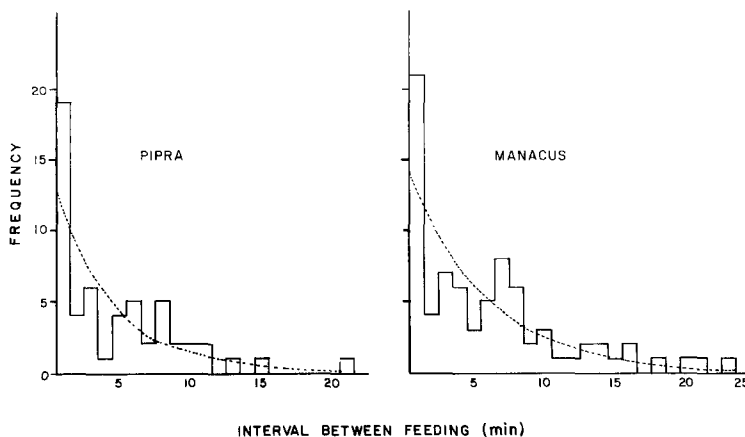


Fig. 4. Frequency distribution of waiting times between individual fruits consumed compared to a random distribution. A negative exponential (dashed line; for *Pipra*, $n=55$, $X=4.8$ min; for *Manacus*, $n=78$, $X=6.1$ min) does not fit observed frequencies of feeding intervals (Goodness of fit test, $P<0.001$)

that fruit consumption did not follow a random temporal pattern (Fig. 4). The frequency distribution of intervals between feeding deviated from a random distribution (negative exponential) due to the occurrence of many more short and long intervals than expected. The birds in captivity filled their guts rapidly, then paused before the next meal. This behavior was also observed in free-living birds; wild *Manacus* fed in short bouts (up to 2 min) approximately every 20 min. Coupled with the gut evacuation data above, this timing implies that manakins wait for their guts to empty before initiating feeding.

Meal size was limited by the degree of gut evacuation. For *Manacus*, the time to the next meal was a function of the size of the preceeding meal (F -test, $F_{(1,21)}=10.585$, $P<0.005$). In *Pipra*, the time preceeding a meal predicted the size of a meal (F -test, $F_{(1,26)}=7.592$, $P<0.025$).

Fruit characteristics influencing fruit consumption

When energy concentration in a fruit species was low, the manakins ate significantly more fruit pulp (Fig. 5, F -test, $F_{(1,20)}=10.0$, $P<0.005$). The highest rate of fruit intake

recorded was 2.8 g wet pulp per hour for *Manacus* and 2.5 g wet pulp per h for *Pipra*.

Two species of fruit for which pulp intake rate by manakins was especially low, *Coccoloba manzanillensis* and *Dolichocarpus dentata* (see three points in the right-hand portion of the bracketed area in Fig. 5), were also fruit with large seeds in which seeds were regurgitated rather than defecated. The birds waited to regurgitate the seed of each fruit before consuming another fruit, and this reduced the rate of pulp intake compared to fruits of similar energetic value.

Thin-pulped, fleshy fruits, such as *Psychotria horizontalis*, contain relatively more non-nutritive seeds, so that each meal has relatively less pulp, reducing the rate of energy yield. *Psychotria horizontalis* (see two points near the left side of the bracketed area in Fig. 5) had a higher proportion of seed per fruit than either *P. marginata* or *P. deflexa*, species of similar energy density (Table 1). Eliminating the points in brackets, associated with regurgitation or high seed density, from the analysis strengthened the predictive value of pulp energy concentration on fruit consumption rate ($R^2=30.2\%$ with points in brackets, $R^2=79\%$ without the points in brackets).

Table 6. The ranges of digestive efficiency (energy assimilation) and gut transit time as a function of diet. Diets are listed in order of increasing gut transit time. Mean digestibilities calculated from mean digestibility for each bird species on that diet (n =number of bird spp)

Diets of birds		Gut transit time (h)	Energy assimilation (%)		References
			Range	Mean \pm SE (n)	
Frugivores	(pulp only) tropical	0.2–1.5	37–85	62.5 \pm 1.5 (2)	24, 27
	temperate	0.3–3.0	41–90	66.6 \pm 5.4 (11)	9, 19, 20, 21, 26, 28
Nectarivores	(sugar solutions)	0.5–0.8	97–99	98.1 \pm 0.4 (4)	3, 7, 13, 23
Insectivores	(adult insects)	0.5–7.4	66–90	75.0 \pm 4.6 (4)	8, 14, 19, 28
Granivores	(seeds)	1.0–10	49–89	75.6 \pm 4.6 (4)	1, 5, 9, 14, 15, 19
	(fruit)	0.5–5.8	62	62.0 (1)	
Herbivores	(grain)	1.3–12.3	73–82	71.5 \pm 5.0 (5)	2, 4, 6, 7, 12, 14, 17, 18
	(grass)		22–54	28.3 \pm 1.3 (4)	
	(fruit)		47–81	60.2 \pm 10.6 (3)	
	(browse)		31–45	35.8 \pm 3.0 (6)	
Piscivores	(fish)	20–70	78–82	79.4 \pm 1.8 (4)	11, 14, 25
Carnivores	(whole vertebrates)	23–72	68–87	76.1 \pm 2.6 (7)	5, 10, 14, 22

Data from: 1) West and Hart 1966, 2) Pulliainen et al. 1968, 3) Hainesworth and Wolf 1972, 4) Moss 1973, 5) Willson and Harneson 1973, 6) Evans and Dietz 1974, 7) Hainesworth 1974, 8) Ricklefs 1974, 9) Walsberg 1975, 10) Duke et al. 1976, 11) Cooper 1978, 12) Robel et al. 1979, 13) Collins et al. 1980, 14) Warner 1981, 15) Ziswiler 1981, 16) Robbins 1983, 17) Halse 1984, 18) Herd and Dawson 1984, 19) Herrera 1984, 20) Sorenson 1984, 21) Johnson et al. 1985, 22) Campbell and Koplin 1986, 23) Karasov et al. 1986, 24) Levey 1986, 25) Speakman 1988, 26) Studier et al. 1980, 27) Worthington, this study, 28) Worthington, unpubl. data

Discussion

The digestive system of manakins is adapted for processing large volumes of fruit, that is, for bulk feeding. Rapid gut transit time, selective regurgitation of bulky seeds, and high assimilation of nonstructural carbohydrates enable the birds to process a large volume of fruit per unit time. These adaptations allow manakins to extract sufficient nutrients from fruit, which typically has low nutrient density, high water content and bulky seeds.

These adaptations are typical of other fruit-eating birds. Passage of seeds through the gut is short in frugivores: Phainopepla (12–45 min, Walsburg 1975), European blackbird (25–50 min, Sorenson 1984), American robin and hermit thrush (15–30 min Worthington unpubl. data) and many other temperate (20–90 min, Herrera 1984; Johnson et al. 1985) and tropical (9–107 min, Levey 1986) frugivores. Levey (1986) found that duration of seed retention was a function of body size, with smaller birds (12–18 g) defecating seeds sooner than larger birds (30–42 g). Time to regurgitate seeds is very rapid (7–19 min) in frugivores (Sorenson 1984; Johnson et al. 1985; Levey 1986; Worthington, unpubl. data).

While frugivorous birds process fruit very rapidly, they show assimilation efficiencies as high as those of birds adapted to feed on other foods (Table 6). The highest digestive efficiencies are found in nectarivores (97–99%) and the lowest are found when herbivores feed on grass (22–54%). Frugivores show a broad range of digestive efficiencies depending on fruit species (37–84%, manakins; 47–83% European blackbirds, Sorenson 1984; North American migrants 44–83%, Johnson et al. 1985). The range of gut transit times within a diet type (Table 6) probably reflect the size of birds tested within that diet type since gut capacity and intestine length are proportional to body size (Calder 1984).

If gut capacity is proportional to body weight and energy demand is proportional to metabolic weight ($\text{Mass}^{0.75}$), one should expect the smaller frugivore to need a faster rate of passage to obtain its energy requirement. Manakins are among the smallest frugivores, and yet they achieve the same assimilation efficiencies as larger frugivores whose gut transit times are relatively longer. In manakins, it appears that the usable energy in food is rapidly assimilated. When fed sucrose solutions, hummingbirds and honeyeaters are 97–99% efficient in assimilating sugars (Hainesworth 1974; Collins et al. 1980). Manakins are nearly as efficient as these nectarivores in extracting accessible, soluble carbohydrates in fruit (TNC assimilation: 86–98%).

Characteristics of fruit which influence assimilation

Do any characteristics of the fruit species account for the wide range of observed digestive efficiencies (37–84% depending on type of fruit)? One hypothesis is that since fruits vary in their nutritional content, a higher assimilation reflects a higher nutrient content of that fruit. However, neither energy content, nor nitrogen content of the fruit was correlated with the digestive efficiency of either bird species. Assimilation of nonstructural carbohydrates was consistently high (86–98%) no matter what the fruit species but energy assimilation was not correlated with TNC content of the fruit either. Therefore the energy content of a fruit tells us little about what proportion is useful to the animal. Johnson et al. (1985) also found that digestive efficiency in temperate frugivores was not correlated with fruit nutrients (lipids, nitrogen, sugars, cations) or energy content.

An alternative hypothesis which might explain the variance in energy assimilation is that these fruits varied in characteristics that influence gut transit time: fruit (meal) size, water content, and particle (seed) size. Warner (1981)

suggests that high water content, small particle size, or high rate of food intake can speed passage of food through the gut and therefore reduce the time for absorption of nutrients and energy. In contrast, Moermond and Denslow (1986) report that high water content in fruits aids nutrient assimilation. I tested for correlation of energy assimilation with each of these factors and found no significant relations.

Implications to foraging ecology

Based on the manakins' digestive adaptations, one can make predictions about fruit choice of wild manakins. The ability to eliminate bulky seeds fast, through regurgitation, can serve to increase food intake rate. European thrushes appear to prefer fruits which have large seeds that can be regurgitated, which enables them to increase fruit pulp consumption (Sorenson 1984). However, since manakins must wait to regurgitate a very large seed (>7 mm maximum dimension) before consuming another fruit (see also Levey 1987b), the time to regurgitate a large seed can reduce the overall rate of fruit consumption. For example, a manakin could consume a maximum of only 100 large-seeded fruits in a day (720 min in a day and 7 min to wait for regurgitation in order to eat again). In contrast, a manakin could consume nearly 1000 fruits per day if it did not wait for regurgitation (Worthington, unpubl. data). Large-seeded fruits (>7 mm) should be rare in the manakin diet if manakins chose fruit to maximize pulp intake. At some point (<2–3 mm) seeds are too small to regurgitate and must pass through the gut (Levey 1987b, Worthington, unpubl. data). If manakins attempt to maximize the amount of pulp passing over the gut's absorptive surface, they should select fruits with a high proportion of pulp relative to seed mass.

To maximize energy intake, manakins should select, among fruits with similar proportion of pulp to seed, those with the highest assimilable energy content in the pulp. The total energy content of fruit pulp is not as accurate an indicator of energy value of a fruit to a bird as is the assimilable energy content of that fruit. In this study, dry matter assimilation was as accurate an indicator of the useable energy content of fruit as energy assimilation.

When fruit is available *ad libitum* in a laboratory cage, manakins can adjust their food intake to meet energy needs. Models that optimize energy intake per unit time (Schoener 1971; Pyke et al. 1977; Krebs and McCleery 1984) predict that an animal should always include a high quality item in its diet no matter how rare the item is and that a low quality item should be ignored no matter what its relative abundance. For manakins, an abundant but low quality fruit may be as energetically valuable per unit time as a rare, high quality fruit, since manakins can double their gut passage rate with increased intake. Such an outcome would be possible if the handling time per individual fruit were insignificant in relation to other time commitments of foraging, e.g., travel time or search time. In that case, eating several low quality fruits may yield as much energy as a single high quality fruit.

My experiments on digestive efficiency show that the manakins can increase energy intake not only by selecting foods with a high assimilable energy concentration but also by increasing the amount of food that passes through the gut. Studies of herbivorous birds suggest that the rate of absorption of any nutrient from the digesta is not limiting

but that the amount of food passed over the absorbing surface could be (Owen 1972, Sibley 1981). Therefore, when faced with fruits of various nutrient contents, manakins could extract the same amount of nutrients in a high or low quality fruit by ingesting more of the poor quality fruits and decreasing gut passage time.

The suite of characteristics that allow manakins to process large volumes of fruit to extract required nutrients may have evolved to meet the characteristics of a fruit diet (low nutrient density, high water content and seeds) or to meet the vagaries in the abundance and diversity of fruits. Manakins experience seasons where fruit abundance is low or the range of selection is small (M. Foster 1977; R. Foster 1982a, b; Worthington 1982, 1989). Manakins are capable of selective feeding in the laboratory (Levey et al. 1984; Moermond and Denslow 1983) but may not have that chance in the field. Their flexible digestive physiology allows manakins to harvest fruits of widely varying quality with equal efficiency.

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