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

Andrea H. Worthington *
Department of Zoology, University of Washington, Seattle, WA 98195, USA

**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 (Belovsky 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 content, 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
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 x 45 x 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 sub-samples was generally less than 1%. Samples of fruit pulp and excreta were analyzed for only 7 fruit species fed to Manacus (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 amount of ripe fruit available and the amount of ripe fruit ingested. 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 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.

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,

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\text{% energy assimilation} = 100 \times \frac{K_i - K_e}{K_i},
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where \(K_i\) = energy ingested (kJ per g dry pulp x g dry pulp ingested) and \(K_e\) = energy excreted (kJ per g excreta x 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.

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