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# NEOTROPICAL AVIAN FRUGIVORES: PATTERNS OF BEHAVIOR, MORPHOLOGY, AND NUTRITION, WITH CONSEQUENCES FOR FRUIT SELECTION

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**ABSTRACT.** A large number of neotropical bird species in many families regularly eat fruit. We discuss the physiological, morphological, and behavioral adaptations associated with eating fruits. Fruits present a number of difficulties for the frugivores, such as the low protein to calorie ratio, the watery bulk, and the undigestible seed mass. Although we find no consistent morphological adaptations for digesting fruits, we show that important adaptations in digestive physiology are to be expected. Both large and small birds have similarly diverse diets, but small birds, such as tanagers and manakins, eat mainly small, carbohydrate-rich fruits, while large species, such as cotingas and toucans, eat a wider range of fruit sizes including both small, carbohydrate-rich fruits and large, lipid-rich fruits.

Most fruit-eaters have large gapes, and many birds swallow fruits whole, although a number of bird species, both small and large, may facultatively eat some large fruits piecemeal. Tanagers and some emberizid finches generally eat fruits by mashing the pulp, swallowing the pulp, juices and small seeds, but dropping medium and large seeds. Birds that take fruits on the wing usually have short, wide, flat bills, whereas those that reach fruits from perches often have long and narrow bills. Differences in bill structure affect the manner of fruit handling and may influence fruit selection.

Most species take fruits either primarily on the wing or primarily from perches. We divide these two general foraging methods into four foraging maneuvers on the wing (hovering, stalling, swooping, and snatching) and three foraging maneuvers from a perch (picking, reaching, and hanging). These foraging techniques differentially affect access to fruits. Differences in flight maneuvers are associated with differences in wing-loading, wing aspect ratio, and degree of slotting. Likewise differences in ability to reach fruit from a perch are correlated with differences in tarsus shape and leg musculature. Very few birds are able to reach fruits well and also pluck them expertly on the wing.

The dichotomy of frugivorous birds into specialists and generalists, with only a couple exceptions, is not supported by comparison of diet, behavior, morphology, or function as dispersers. The important differences among fruit-eating birds depend on the constraints of morphology on behavior. Differences in digestive systems, bill strength and shape, wing and leg morphology, and body weight differentially affect the accessibility of fruits, the ease with which they are handled, the rate at which they are eaten, the efficiency with which they are digested, and thus influence which fruits are selected. The presence of fruit-eating birds in so many families is not evidence for lack of requirements for eating fruits but rather represents adaptive specialization to exploit fruits displayed in different ways.

**RESUMEN.** En las zonas neotropicales se encuentran un gran numero de especies de aves pertenecientes a numerosas familias cuya dieta consiste de frutas. Presentamos una discusión sobre las adaptaciones fisiológicas, morfológicas y de comportamiento que están asociadas con la costumbre de comer frutas. El comer frutas le presenta una serie de problemas a aves frugívoras como por ejemplo: una relación baja entre proteínas y calorías, un gran volumen de materia acusa y la presencia de semillas indigeribles. Aunque no encontramos adaptaciones digestivas morfológicas generales para comer frutas, demostramos que adaptaciones digestivas fisiológicas en aves frugívoras son de esperarse. Las aves frugívoras, tanto las grandes como las pequeñas, tienen dietas similares en cuanto a la diversidad de frutas. Sin embargo, las aves pequeñas, como las tangaras y los saltarines, se alimentan mayormente de frutas pequeñas que son ricas en carbohidratos; mientras que las aves de mayor tamaño, como las cotingas y los tucanes, se alimentan de frutas de diversos tamaños; tanto de frutas pequeñas ricas en carbohidratos, como de frutas grandes ricas en lípidos.

La mayoría de las especies frugívoras tienen un rictus ancho y muchas ingieren la fruta entera sin despedazarla. Sin embargo, algunas especies, tanto grandes como pequeñas, tienen la capacidad facultativa de comerse la fruta trozo a trozo. Las

tangaras y algunos de los pinzones usualmente se comen la fruta después de aplastarla con el pico. Usando este método ellos ingieren la pulpa, el jugo y las semillas pequeñas, pero rechazan las semillas grandes y medianas. Las especies que obtienen la fruta volando, generalmente tienen picos cortos, anchos y de poca profundidad. Mientras que las que obtienen la fruta desde una perchta comúnmente tienen picos largos y estrechos. Estas diferencias en la estructura del pico afectan la manera en que el ave manipula la fruta y pueden influenciar el proceso de selección entre diferentes frutas.

La mayoría de las especies usan uno de dos métodos principales para obtener las frutas, las toman volando o las toman desde una perchta. Para las especies que obtienen las frutas volando, dividimos las maniobras de forrajeo en cuatro categorías: "hovering," "stalling," "snatching" y "swooping." Para las especies que obtienen la fruta desde una perchta, dividimos las maniobras de forrajeo en tres categorías: "picking," "reaching" y "hanging." Todos estos métodos de forrajeo afectan de manera diferente el acceso que un ave pueda tener a una fruta. Las diferencias en maniobras de vuelo están asociadas con diferencias aerodinámicas como el "wing-loading," "wing aspect ratio" y el grado de "slotting." De igual manera, las diferencias entre las especies en la habilidad de alcanzar frutas desde una perchta están asociadas con diferencias en la forma del tarso y la musculatura de las patas. Son muy pocas las especies que tienen la capacidad de obtener frutas desde una perchta fácilmente y a la misma vez poder tomar frutas en vuelo con destreza.

La dicotomía existente entre aves frugívoras "especialistas" y aves frugívoras "generalistas" no está apoyada por nuestras comparaciones de las dietas, comportamientos, morfologías, o la función de las especies como dispersoras de semillas. Las diferencias más importantes entre las aves frugívoras se basan en las restricciones impuestas por la morfología y el comportamiento del ave. Diferencias en el sistema digestivo, la fuerza y configuración del pico, la morfología de las patas y alas y el peso del ave afectan de la manera diferente la accesibilidad de las frutas, la facilidad con que se manipulan, la rapidez con que se ingieren y la eficiencia con que se digieren y por lo tanto, influyen de manera muy importante en el proceso de selección entre diferentes frutas. La presencia de tantas aves frugívoras pertenecientes a numerosas familias no representa una evidencia de que no se necesitan adaptaciones para comer frutas, si no demuestra numerosas especializaciones adaptivas para explotar frutas que están presentadas en maneras diferentes.

Fruit-eating among tropical birds is so wide-spread as to make definition of "frugivorous" difficult. Few species are so restricted to fruits that their nestlings are completely reared on fruits (Morton 1973). Oilbirds (*Steatornis caripensis*, Snow 1961, 1962c) and Bearded Bellbirds (*Procnias averano*, Snow 1970) are in this category. At the other extreme are the many primarily insectivorous birds that exploit the abundant fruits of some trees (e.g., Eisenmann 1961; Olson and Blum 1968; Morton 1971; Leck 1972a, 1973; Howe and DeSteven 1979) or take an occasional fruit while foraging for insects. Traylor and Fitzpatrick (1982) noted for flycatchers (Tyrannidae) that while fruit features heavily in the diets of only a few species, nearly all eat some fruit occasionally. The same is probably true of woodpeckers, and even rails have been observed taking fruits in Costa Rica (*Aramides cajanea* feeding on low growing Melastomataceae berries, D. J. Levey, pers. comm.; *Porphyrrula* feeding on *Heliconia* fruits, Skutch 1933). Between these extremes are birds whose diets consist of some mixture of fruits and insects and occasionally vertebrates, snails, or leaves (Jenkins 1969; Morton 1978; Stiles 1983).

Here we use the word "frugivore" for birds whose diets include a substantial portion of fruit at least during some seasons, rather than confining it to birds that eat solely fruits. Nearly all of the so-called frugivorous birds eat other types of foods as well (usually insects or other invertebrates) and should be properly referred to as omnivores. However, the term "frugivore" has been commonly used for such frequent but not exclusive fruit-eaters as tanagers. Here we use the terms "frugivore" and "fruit-eater" interchangeably.

Adaptations of fruits that enhance seed dispersal by birds have been described in detail (Ridley 1930; van der Pijl 1969). The most obvious common characteristic is an energy or nutrient reward in the form of a soft, fleshy pulp surrounding the seed. In addition, bright colors and/or morphological modifications presumably advertise the presence of the reward (Morden-Moore and Willson 1982; Willson and Thompson 1982; Janson 1983). The seed itself is frequently provided with some form of protection that reduces the probability of destruction by the bird or discourages invertebrate seed-eaters, e.g., hard seed coat or toxins in the seed, seed coat, or fruit pulp (Herrera 1982). Given that fruits, especially small-seeded,

sweet, berry-like fruits, are at times abundant, visible, and easily accessible, it is not surprising that many birds occasionally exploit this ready source of energy.

Morphological adaptations for fruit-eating in birds have not been so clearly identified. The most commonly cited examples concern a relatively large gape (Snow 1973) and lack of crop or muscular gizzard. Even these modifications of the gut may not be typical (see Morphology of the Digestive Tract below). Some species exhibit behavioral adaptations, such as regional or elevational migrations that track local fruit abundances (e.g., Fogden 1972; Crome 1975a, c; Morton 1977; Karr et al. 1982; Wheelwright 1983; F. G. Stiles, pers. comm.). Most fruit-eating birds do not specialize on one or a few species of fruits and dietary overlap among many fruit-eating birds is broad (e.g., Snow and Snow 1971; Leck 1971b; Crome 1975a), especially with respect to small-seeded fruits (Eisenmann 1961; Land 1963; Willis 1966; Olson and Blum 1968; Leck 1973; Howe 1981, 1982).

In contrast to this general picture is the persistent notion of frugivores arrayed on a continuum between specialists and generalists (McKey 1975; Howe and Estabrook 1977; Snow 1980). The idea is based on the assumption that reliable attraction of dispersers to large-seeded fruits entails provision of a high quality reward to the bird. Hence, large-seeded fruits are seen to be nutritious and closely linked evolutionarily with highly frugivorous birds that depend on fruits for most of their protein and energy needs (hence specialists) and whose gapes are large enough to handle large seeds (Snow 1971a; McKey 1975). These birds are also seen to provide high quality dispersal, i.e., they preferentially feed on these large fruits and disperse the seeds away from the parent plant. The seeds are not destroyed. Most small, fruit-eating birds are seen as opportunists (generalists) that take fruits nonselectively as they are encountered and are willing to settle for small, juicy, low-reward fruits (McKey 1975; Howe and Estabrook 1977).

However, there is no reason to expect that fruit specialists provide a higher quality dispersal than generalists (Wheelwright and Orians 1982), and we shall show that the diets of specialists and generalists often have much in common. Our own studies of Costa Rican fruit-eating birds have suggested that fruits displayed in different ways are differentially accessible to birds that forage in different ways (Moermond and Denslow 1983; Denslow and Moermond, in press). Here we compare frugivores with respect to fruit choices, fruit handling, and foraging behavior and suggest that these factors form a more functional basis on which to categorize this phylogenetically and morphologically diverse group of birds.

#### WHO EATS FRUITS

Neotropical fruit-eating birds are found among a broad variety of bird families. Very few eat only fruits as adults and nestlings. Most supplement their fruit diets with different, relatively protein-rich foods, and those that do feed almost exclusively on fruits as adults usually feed insects to their young. The nature of these alternative protein sources—seeds on one hand and insects or vertebrates on the other—provides a convenient basis for classifying frugivores.

*Seed-eating frugivores.*—That relatively few species combine a diet of seeds and fruit pulp is not surprising in view of the different digestive apparatus necessary for processing the two foods. Granivorous birds are characterized by large crops, muscular gizzards, long small intestines, and slow passage rates through the digestive tract in contrast to frugivores (Ziswiler and Farner 1972). Many fruit-eaters in this category are, in fact, feeding on both seed and pulp of fleshy fruits. They are often seed destroyers, rather than dispersers, and generally prefer green (unripe) or partially ripe fruits to fully ripe fruits in which the seed coats are likely to be fully hardened. Most also supplement their diets with young leaves, shoot tips, buds, and occasional insects.

*Columba* pigeons swallow seeds and berries whole; large seeds especially are undoubtedly destroyed in the large, muscular gizzard, although very small seeds, such as those of *Cecropia*, *Ficus*, or *Miconia*, may pass through intact. The bill is relatively weak and only very soft fruits can be eaten by biting or tearing out chunks (Goodwin 1970). New World parrots are also primarily seed-eaters that break up seeds with their bills before swallowing (Forshaw 1978; Howe 1981; Janzen 1981). The woody husks surrounding arillate seeds of many canopy tree fruits may offer some measure of protection from such seed predators.

The Cracidae also subsist largely on fruits and seeds. Curassows (*Crax*, *Nothocraix*) are primarily terrestrial foragers that feed on fallen or low growing, unripe fruits (Delacour and Amadon 1973). Crop and gizzard are well-developed, so many seeds are probably digested in addition to the fruit pulp. Chachalacas (*Ortalis*) and guans (*Penelope*) are primarily arboreal

and forage on ripe fruits (Delacour and Amadon 1973). Long legs and neck facilitate reaching of fruits on small diameter, pendent twigs. The gizzard is thin-walled and the crop is poorly developed, so most seeds probably pass through the gut intact.

Finches in the subfamilies Emberizinae and Cardinalinae feed primarily on seeds, but some cardinalines, especially *Saltator* spp. and the grosbeaks (e.g., *Caryothraustes*, *Pytilius*, and *Passerina* (*Cyanocompsa*) *cyanoides*), eat a substantial amount of fruit as well. All include insects in their diets, and saltators are also known to feed on young leaves (Jenkins 1969; pers. observ.). The size and hardness of a seed probably influence how it is handled. Seeds of *Heliconia* spp. (Musaceae) are too hard for even the heavy-billed *Passerina cyanoides* to break (Stiles 1979, pers. observ.), but both *P. cyanoides* and *Caryothraustes poliogaster* will crack the smaller seeds of *Psychotria brachiata* (Rubiaceae). Saltators appear to digest very few seeds and supplement their diets primarily with insects (Jenkins 1969). The fruit-eaters in this group crush the fruit pulp before swallowing (Moermond 1983). Large seeds are frequently dropped in place if not eaten and, therefore, poorly dispersed, whereas small seeds may be swallowed intact (Moermond and Denslow, unpubl. data; D. J. Levey, pers. comm.).

*Insect-eating frugivores*.—Most fruit-eating birds eat some insects and provide them to young nestlings. Like frugivores, primarily insectivorous birds have thin-walled gizzards and small crops (Cvitanic 1970). Passage rates through the digestive tracts of the two groups are comparable (Ziswiler and Farner 1972; Herrera 1984). Incorporation of fruits into the diet of an insectivore is apparently done as readily as is the reverse. Frugivores frequently take advantage of locally superabundant insect populations (Eisenmann 1961), and some migrants, e.g., *Dendroica castanea*, *D. pensylvanica*, and *Vermivora peregrina* are insectivorous on their temperate breeding grounds but often highly frugivorous in the tropics (articles in Keast and Morton 1980). In fact north temperate migrants may be important dispersers of seeds of some neotropical trees (Leck 1972a; Howe and DeSteven 1979; Howe and Vande Kerckhove 1980; Greenberg 1981). Except during seasons of low fruit abundance when partially ripe fruits are taken (Foster 1977), insect-eating frugivores prefer fully ripe fruits to partially ripe fruits (Moermond and Denslow 1983). Most take both watery, sweet fruits and dry or oily fruits. Fruit-eating birds in the following families supplement their fruit diets with insects and, occasionally, small vertebrates: Cotingidae, Pipridae, Tyrannidae, Muscicapidae (Turdinae), and Emberizidae (including Parulinae, Icterinae, Thraupinae, and Cardinalinae).

## NUTRITION AND DIGESTION

### FRUIT AS A FOOD RESOURCE

Pulp quality varies widely with respect to amount, carloric and nutrient contents, digestibility of the pulp (fiber, water content), seed size and total bulk of seeds, toughness of fruit coat, and presence of secondary compounds (e.g., phenols and alkaloids, Herrera 1982). Seeds ingested with the pulp may add considerably to the non-digestible bulk of the fruit (e.g., commonly more than 50 percent of the total fruit weight for few-seeded fruits but much less for fruits with many small seeds, White 1974; Snow 1981; Wheelwright et al. 1984). In contrast to both seeds and insects, fruits are generally low in protein and in lipid and may be high in carbohydrate (Table 1). A survey of families producing bird-dispersed seeds (Table 1) also reveals that in general fruits are either rich in lipid or in carbohydrate. Only in a few instances does a fruit contain more than 20 percent each of lipid and carbohydrate. The median protein content for 29 tropical families of bird-dispersed fruits is 8.4 percent of the dry weight of the fruit pulp (Table 1) compared to averages of approximately 12 percent for 12 species of cereal seeds (Jenkins 1969) and 66 percent for 19 species of insects (White 1974). Among these fruits, there is no correlation between lipid and protein content of fruit pulp (Spearman  $R = 0.182$ , n.s.).

The water content of fruits is generally very high, contributing to the impression that fruits are an extremely low quality food source. Experimental diets fed to granivores are low in moisture (about 11%) in comparison to fruits (50% to 94%, Table 1). On a dry weight basis, the protein contents of many fruits are only slightly less than those of seeds, and nutrients are easily assimilated from an aqueous solution. Fruit pulp is also generally low in fiber, requiring little mechanical reduction to render the cell contents accessible to digestive processes. Fruits thus are characterized by a bulky, dilute pulp coupled with a substantial portion of undigestible seed mass that must also be handled. It is apparent that efficient handling of a bulky food is one of the major constraints on a bird dependent on fruits for a large portion of its energetic and nutritional needs. One solution for the birds is a rapid gut passage time

TABLE 1  
ENERGETIC AND NUTRIENT CONTENTS OF FRUITS IN TWENTY-NINE PLANT FAMILIES THAT USE  
BIRDS AS SEED-DISPERERS<sup>1</sup>

	No. species sampled	Water %	Protein <sup>2</sup>	Lipid	Carbohydrate	kcal/g <sup>3</sup>	P/C <sup>4</sup>	Source <sup>5</sup>
Annonaceae	1	86	4.8	3.3	21.0	1.40	.034	8
Araliaceae	1	68	12.0	33.0	55.0	5.83	.020	7
Apocynaceae	2	73	11.0	17.3	4.5	2.35	.047	6
Boraginaceae	2	80	16.8	5.2	68.1	3.96	.042	3, 7
Burseraceae	4	85	11.0	3.9	65.0	3.53	.031	1, 7
Connaraceae	1	79	8.4	15.9	70.3	4.72	.018	7
Flacourtiaceae	1	90	5.7	.9	37.8	1.89	.030	8
Lauraceae	24	68	6.2	25.3	9.0	3.03	.020	1, 2, 8
Leguminosae	1	56	1.9	22.7	73.2	5.14	.004	7
Loranthaceae	1	55	5.8	52.7	38.1	6.73	.009	7
Malvaceae	1	56	3.1	0.3	35.2	1.60	.019	8
Melastomataceae	2	66	4.2	6.8	84.0	4.21	.010	7
Meliaceae	1	54	15.1	59.7	22.3	7.23	.020	9
Moraceae	4	78	6.4	4.3	79.0	3.89	.016	3, 7
Musaceae	1	74	10.6	39.2	40.4	5.81	.018	7
Myrsinaceae	2	87	6.0	2.7	53.8	2.71	.022	5, 8
Myristicaceae	1	55	2.5	63.0	9.0	6.35	.004	4
Myrtaceae	2	81	4.5	1.6	53.8	2.53	.018	7, 8
Ochnaceae	1	57	4.9	11.0	81.0	4.52	.011	7
Olacaceae	1	68	17.5	17.6				7
Palmae	4	85	9.5	20.8	66.6	4.88	.027	1, 7
Phytolaccaceae	1	80	1.9	2.4				7
Rosaceae	3	80	6.5	1.5	38.0	2.00	.032	3, 8
Rubiaceae	2	87	13.2	5.2	74.6	4.14	.032	7
Rutaceae	1	77	8.8	1.2				8
Sapindaceae	1	83	9.9	3.2	82.5	4.11	.024	7
Solanaceae	1	89	9.2	1.3	15.6	1.22	.075	8
Verbenaceae	3	80	2.2	2.2	38.4	1.86	.012	7, 8
Zingiberaceae	1	92	17.9	1.8	60.9	3.54	.051	7
Medians		79	6.5	5.2	53.8	3.92	.020	
		(n = 29)	(n = 29)	(n = 29)	(n = 26)	(n = 26)	(n = 26)	

<sup>1</sup> Median values are provided when data for more than one species per family are available. Except for water, all percents are based on dry weights.

<sup>2</sup> Protein was calculated as  $4.4 \times$  percent nitrogen (Milton and Dintzis 1981).

<sup>3</sup> The following conversion factors were used to estimate calorific content: protein 5.2 kcal/g; lipid 9.3 kcal/g; carbohydrate 4.0 kcal/g (Watt and Merrill 1963).

<sup>4</sup> Protein : calorie ratio is calculated as % protein/kcal·kg<sup>-1</sup> food.

<sup>5</sup> Sources: 1 = Snow 1962c; 2 = Snow 1981; 3 = Munzell et al. 1949; 4 = Howe and Vande Kerckhove 1980; 5 = M. Foster 1977; 6 = McDiarmid et al. 1977; 7 = White 1974; 8 = Wheelwright et al. 1984; 9 = Foster and McDiarmid 1983.

(Groebels 1932; Walsberg 1975; Herrera 1984). Another solution is for the birds to select fruits with low proportions of undigestible matter. Studies by Howe and Vande Kerckhove (1980) and Herrera (1981) have shown that birds prefer fruits with a large pulp to seed ratio (at least among large-seeded fruits), and Sorensen (1984) correlated fruit preference in *Turdus merula* with fruits whose seeds are regurgitated rather than defecated. Regurgitated seeds have significantly less residence time in the gut.

Although yearly extremes of fruit abundance may commonly differ only two-fold (Fogden 1972) compared to many-fold in temperate habitats, seasons of fruit abundance may nevertheless be well-defined even in aseasonal wet tropical climates (Snow 1965; Janzen 1967; Smythe 1970; Frankie et al. 1974; Hiltz 1980; Foster 1982a). Fruiting seasons may show marked year-to-year variation (Ward 1969a; Fogden 1972; Foster 1982a, b). Trees may fruit on a supraannual periodicity (Frankie et al. 1974), crops of some species may fail completely in some years (Crome 1975a; Foster 1982b; Faaborg and Terborgh 1980), and some species may not fruit consistently at the same time each year (Foster 1982a). Crop sizes, fruit characteristics, spatial distributions, and phenologies of fruit production differ between canopy and understory plants. Understory trees and shrubs are more likely to ripen few, small fruits

over an extended season than are canopy trees (Frankie et al. 1974; Hilty 1980; Opler et al. 1980).

Thus, even though fruits appear to be common year round in rain forest, suitability of fruits for a particular frugivore may differ, and favored fruits may be patchily distributed in space (Snow 1962c; Fogden 1972) and poorly predictable in time. The tracking and exploitation of a locally variable but sometimes abundant food source (for example by flocking, Leck 1971a; Buskirk 1976) is then another important attribute of a frugivorous habit.

#### NUTRITIONAL CONSTRAINTS ON FRUGIVORES

Unfortunately, studies on the nutritional requirements of frugivorous birds are scarce. We are often limited to extrapolations from studies on granivores—chickens, domestic pigeons, and sparrows—the results of which may be of limited value in understanding digestive physiology of frugivores. Nevertheless, some general patterns are suggested.

Studies of temperate bird species suggest that ingestion is limited primarily by energetic requirements (Fisher 1972) and (to some extent) volumetric constraints (chickens, Hill and Dansky 1954; Tree Sparrows, *Spizella arborea*, Martin 1968). For primarily carnivorous, insectivorous, or granivorous birds, other nutritional requirements such as protein and minerals are likely to be largely satisfied at the same time that energetic requirements are met if there is variety in the diet.

Studies of adult birds suggest that a diet of 4 percent to 8 percent protein (fresh weight) is necessary for maintenance (chicken = 7%, Leveille and Fisher 1958; *Spizella* = 8%, Martin 1968; and papers reviewed by Berthold 1976a). Martin (1968) found that although a diet of 4 percent protein was minimal for survival of *Spizella arborea*, assimilation efficiencies of nitrogen and carbohydrate are significantly greater in diets containing at least 8 percent protein. Initial indications are, however, that protein requirements (or ability to extract sufficient protein from fruits) differ importantly among species. Berthold (1976a) showed clearly that several European passerines (*Sylvia atricapilla*, *S. borin*, *Turdus merula*, and *Erythacus rubecula*) were unable to maintain weight on a diet consisting solely of fruits. The birds consumed adequate amounts of calories but not of protein. In contrast, the waxwing (*Bombycilla garrulus*) maintained weight for 10 to 18 days on a diet consisting solely of berries (Berthold 1976b). In another study, the heavily frugivorous *Phainopepla nitens* maintained weight on a diet of mistletoe berries, but the house finch (*Carpodacus mexicanus*) did not (Walsberg 1975). These studies suggest that there are important constraints on the digestive physiology of birds dependent on fruits for the majority of their calorie and nutrient requirements. Although many species may exploit fruits on an occasional basis, dependence on fruits for longer periods of time may not be so easily accomplished.

For adults of many frugivores, protein and calorie levels of many fruits are adequate providing that sufficient quantity can be processed daily. We have kept tropical birds of families Emberizidae (tanagers and finches), Pipridae, Troganidae, and Ramphastidae, and temperate birds in the Turdinae, Bombycillidae, and Mimidae on a synthetic diet for several months during which time their weights stayed close to or above capture weight. The content of this diet was richer than that of many tropical fruits: 86 percent water; 13 percent protein; 6 percent lipid; 78 percent carbohydrate by dry weight. Consistent with Walsberg's study, the three exceptions that required an additional protein supplement to maintain weight were all seed-eating finches—*Arremon aurantiirostris*, *Caryothraustes poliogaster*, and *Passerina (Cyanocompsa) cyanoides* (Moerman and Denslow, unpubl. data; D. J. Levey, pers. comm.). The other species did well on the diet and, although we do not know whether they could have reproduced, they were able to molt. Caged temperate frugivores maintained solely on our synthetic diet ingested between 1.8 and 2.2 g (fresh weight) of food per gram of body weight per day in comparison to 0.2 g food per gram of body weight per day in the case of the granivorous *Spizella* (Martin 1968). A 30 g frugivore must consume approximately 60 g of our artificial diet daily—the volume equivalent to 171 *Ardisia revoluta* fruits (6.0 mm diameter) or 20 *Cinnamomum laubautii* fruits (23.3 × 13.2 mm), including their seeds (data from Foster 1978). In caloric equivalents the numbers of fruits are 287 and 12.2 fruits respectively. A similar pattern has been found for a frugivorous neotropical bat (Morrison 1980).

It is apparent from these estimates that processing time (as opposed to searching or handling time) is likely to be an important component of the foraging equation for frugivorous birds. For birds handling large-seeded fruits with firmly attached pulp (e.g., Lauraceae and Palmae), separation of the pulp from the seed may be an important limitation to processing rate.

Resplendent Quetzals (*Pharomachrus mocinno*) may take an hour to regurgitate the seed from a single large *Beilschmiedia* (Lauraceae) fruit (N. T. Wheelwright, pers. comm.), and Collared Aracaris (*Pteroglossus torquatus*) may regurgitate a single *Ocotea* (Lauraceae) fruit and then reswallow it three times over a period of almost an hour before the pulp is removed from the seed (E. Santana C., pers. comm.). For birds feeding on small-seeded, sugary fruits, physiological specializations that permit rapid absorption of nutrients from dilute aqueous solution are likely to be more important. Studies on starlings (*Sturnus vulgaris*) suggest that unusually high rates of kidney function may be one component of the physiological adaptations of frugivores to their diets (B. Wentworth, pers. comm.).

Digestive adaptations for efficiently processing watery, sweet fruits may constrain the facility with which some frugivores are able to incorporate dry or oily fruits into their diets and at least partially explain the general preference of frugivores for ripe over partially ripe fruits (Foster 1977; Moermond and Denslow 1983). Preliminary data suggest that the watery texture of fully ripe fruits allows them to be more efficiently assimilated although unripe fruits may also contain higher levels of digestion inhibitors such as tannins. Caged Collared Araçaris thoroughly digested nearly all fully ripe *Hamelia patens* (Rubiaceae) fruits offered but digested a significantly lower proportion of partially ripe fruits (Santana C., Moermond, and Denslow, unpubl. data).

Differences in physiological treatments of proteins and carbohydrates impose further constraints on the nutrition of frugivores. Assimilated protein can be converted to fat, stored as protein in muscles (Fogden and Fogden 1979), or burned as an immediate source of energy. Nitrogen in excess of that required for body maintenance, feather production, or reproduction can be excreted. Assimilated lipid and carbohydrate may be burned for energy or stored as fat or glycogen but cannot be excreted. Unless frugivores are unusual in possessing some mechanism by which protein can be differentially assimilated relative to carbohydrate, protein and carbohydrate are probably assimilated with similar efficiencies (about 75%, White 1974).

For these reasons, the protein : calorie ratio (here reported as percent protein : Kcal/100 g food, White 1974) is an important indication of the quality of the diet. The few bird species for which dietary requirements have been determined appear to do best on dietary protein : calorie ratios of approximately .02 to .05 for adults (.039 for laying quail, Nestler et al. 1944; .038 to .052 for laying and breeding chickens, National Research Council 1960; .028 for *Spizella*, Martin 1968). Protein : calorie ratios have been calculated for several tropical fruits (Table 1). Some are considerably lower than the predicted dietary requirements, e.g., lipid-rich Myristicaceae .004; at best the protein : calorie requirements of adult birds can be met only minimally by a random selection of tropical fruits if frugivores have similar protein assimilation and utilization efficiencies as granivores.

The problem of lack of protein is compounded for nestlings and for reproductive and molting adults, which require protein for both maintenance and for new tissue production. During times in which protein demands are high, calories are also likely to be in excess of metabolic needs (Foster 1978). Thus, birds feeding predominantly on fruits must possess some mechanism to deal with excess calories in their diets. For example, young Oilbirds deposit large quantities of fat before leaving the nest even though dietary protein is so low as to prolong the fledgling period much beyond that usual for birds of that size (Snow 1961, 1962c; White 1974). Other neotropical frugivores (e.g., Cotingidae, Pipridae, Thraupinae) do not appear to store large quantities of oil and duration of the nestling period appears to be no longer (on average) than for non-frugivores (Ricklefs 1974).

Walsberg (1975) suggested that frugivores may be less efficient at assimilating calories than granivores, or, alternatively, that the daily energy budgets of birds feeding mainly on fruits may be higher than those for birds supplementing their diets with insects. This appears to be the pattern in bats (D. W. Thomas, pers. comm.), and White (1974) presented evidence that the efficiency of conversion of protein to tissue is about 63 percent in Oilbird nestlings in contrast to 6.8 percent for the insectivore nestlings he studied. Protein is used to meet only 14.2 percent of the metabolic needs of Oilbird nestlings in comparison to 75.5 percent of the needs of insectivorous nestlings. For most nestlings and many adult frugivorous birds, some protein is supplied from insects (Skutch 1954, 1960, 1969; Snow 1962a, b; Snow and Snow 1971; Morton 1980), and fruits are then used primarily as a source of calories. Thus, most birds that are highly or totally frugivorous as adults feed insects to very young nestlings; the proportion of fruits in the diet increases as the nestlings mature, and the ratio of protein to calories metabolized approaches that of adult birds (Morton 1973; White 1974; Skutch 1976;

Wheelwright 1983). White (1974) noted that the ratios of protein to calories metabolized by nestlings of five tropical species were all initially higher than that obtainable from fruits alone, but that this ratio was lower for birds feeding both fruits and insects to nestlings (*Elaenia flavogaster*, *Turdus grayi*, *Zarhynchus wagleri*) than for a total insectivore (*Iridoprocne albilinea*). Oilbirds only bring fruit to nestlings, but the nestlings receive food from the parents with a higher protein : calorie ratio than fruits provide. White (1974) suggested that adults provision the young nestlings with a high protein regurgitated liquid (Snow 1961) analogous to that produced by pigeons.

Nevertheless, for many species, fruits are, at times, an important energy source. In this sense even those species that feed primarily on insects may be obligate frugivores, because fruits provide critical calories, perhaps freeing insect proteins for egg or feather production. The demand for fruits is particularly noticeable during seasons in which few ripe fruits are available. During these times, birds may take green (unripe) fruits (Leck 1972b), greatly increasing the foraging time necessary to acquire sufficient food (Foster 1974, 1977). In a Costa Rican rain forest, we have recorded 15 species of birds eating green or partially ripe fruits during one season of particularly low fruit availability (Moermond and Denslow, unpubl. data).

Reproduction in an adult bird often depends on the level of protein in the diet (Ward 1969a; Fogden 1972; Crome 1975a, b; Fogden and Fogden 1979). Among tropical frugivores, breeding and molting seasons may be closely tied to the quality and abundance of the resource base both for protein and for energetic requirements. In Trinidad the breeding seasons of Oilbirds (Snow 1961) and Bearded Bellbirds (Snow 1970) coincide with the fruiting seasons of Lauraceae, Burseraceae, and Palmae (all of which produce particularly nutritious fruits). In Singapore and Sarawak, Yellow-vented Bulbuls (*Pycnonotus goiavier*) breed during seasons of fruit and insect abundance (Ward 1969b; Fogden 1972).

Fogden (1972) suggested that frugivores may not be sufficiently good at hunting insects to meet both daily metabolic protein requirements and to store sufficient protein for reproduction or feather production on a totally insect diet. Reproduction and molting are, therefore, closely dependent on energy obtained from fruits. Under such circumstances, all protein acquired from insects can then be used to meet protein rather than energetic demands. This thesis is supported in the breeding of *Phainopepla* in the deserts of the southwestern United States. Nesting coincides with abundance of both insects and mistletoe fruits. If either resource fails, nesting is abandoned or not initiated (Walsberg 1977). The breeding seasons of the Black-and-white and the Golden-headed Manakins (*M. manacus* and *Pipra erythrocephala*) in Trinidad coincide with fruiting peaks of Melastomataceae and Rubiaceae, neither of which have notable concentrations of either proteins or lipids (Snow 1962a, b, 1965).

#### MORPHOLOGY OF THE DIGESTIVE TRACT

We expect that the digestive tract of primarily frugivorous birds should reflect a diet of bulky, watery, non-fibrous foods that are generally low in protein, high in soluble carbohydrate, and variable in lipid. As noted above, it would be advantageous for frugivores to process fruit pulp quickly, absorbing only the easily available nutrients from large volumes of fruits. Thus, we expect to find little provision for food storage, short intestines (Pulliainen et al. 1981), non-muscular gizzards (because fruits require little mechanical reduction), and large livers relative to body size (detoxification of the secondary compounds frequently present in fruits (Herrera 1982) occurs primarily in the liver in vertebrates (Brattsten 1979)).

Comparative data on the morphology of the digestive apparatus of predominantly frugivorous birds are not extensive. Moreover, they are complicated by seasonal variation in diets (especially among temperate frugivores), differences in fruit and seed handling behavior, and the nature of alternative sources of protein (e.g., seeds, insects, vertebrates). As Herrera (1984) noted, functional and behavior modifications may be more important components of the evolution of frugivory than less-flexible morphological adaptations. Although some generalizations are apparent, there is considerable variation in the morphology of the digestive tract among fruit-eaters, and some of the generalizations suggested above are not supported. We must await considerably larger sample sizes that take into account diverse feeding ecologies of frugivores.

In most species there appears to be little provision for short-term storage of fruits (but see Ziswiler and Farner 1972). The crop (if present), esophagus, and/or proventriculus are small

(Wetmore 1914; Cadow 1933; Jenkins 1969 and papers described therein; Walsberg 1975). However, the proventriculus is enlarged in *Euphonia*, and the esophagus is extensible in swallow-tanagers (Schaefer 1953). Wheelwright (1983) also reported the presence of an expandable proventriculus in Resplendent Quetzals that presumably accommodates large lauraceous fruits. These birds have no crop, and the esophagus is not used to store food.

The soft, non-fibrous nature of fruit pulp is reflected by the non-muscular gizzard in many frugivores (Cadow 1933; Jenkins 1969 and papers described therein; Walsberg 1975). The quetzal has rings of muscles around the esophagus, presumably to facilitate regurgitation of large seeds, and also a muscular gizzard (Wheelwright 1983). Herrera (1984) found no difference in gizzard size among seed dispersers (all Muscicapidae) and non-frugivores in a Mediterranean woodland. In addition, Herrera (1984) reported no morphological differences between seed dispersers and non-frugivores with respect to liver size or intestine length in relation to body size.

Other studies also have failed to find a consistent pattern of intestine length in relation to body weight of frugivores. Although some authors have suggested that the intestine length in frugivores is short (e.g., Desselberger 1931; Docters van Leeuwen 1954; Ziswiler and Farner 1972; Walsberg 1975), waxwings apparently have long intestines (Cvitanic 1970; but see Walsberg 1977), and Jenkins (1969) reported no consistent pattern among species of Costa Rican frugivores he examined. Intestinal caecae are not common in frugivores, presumably reflecting the non-fibrous nature of their food; however, Wheelwright (1983) described paired caecal sacs packed with fruit skins in the Resplendent Quetzal.

It is apparent that some of the most important adaptations to a fruit-eating habit involve a digestive physiology that can accommodate the processing of a bulky, dilute food that is relatively high in calories in comparison to protein. To some degree these may be reflected in the morphology of the digestive tract, but this structure is also likely to retain elements that maintain the capability of processing other foods and that reflect the phylogenetic affinities of the frugivores, obscuring patterns associated primarily with frugivory. Moreover, fruits do not represent a homogeneous food resource. Important differences among them in source of calories (primarily lipid or carbohydrate), seed number and size, and the firmness with which the pulp is attached to the seed are likely to be reflected in the morphology of the digestive tract and the digestive physiology of birds feeding on fruits.

#### DIET BREADTH AND FRUIT SELECTION

With a few notable exceptions tropical frugivores exploit many species of fruits (Snow 1981; Stiles, in press; Wheelwright et al. 1984). Three species of Costa Rican saltators together included 189 fruit species in their diets (Jenkins 1969). Worthington (1982) recorded 38 species in the diet of *Manacus vitellinus* on Orchid Island, Panama, Snow (1962a, b) observed 66 and 43 species in the diets of two species of manakins in Trinidad, and N. T. Wheelwright (pers. comm.) recorded more than 96 species of fruits in the diets of Emerald Toucanets (*Aulacorhynchus prasinus*). Even Oilbirds, which take few if any insects, use fruits from 37 species of plants during their nesting season (Snow 1962c).

Such data, together with observations of many diverse bird species exploiting abundant crops of some fruiting trees, have been the basis for the hypothesis that some frugivores, especially the small birds that feed on small, berry-like fruits, are not highly selective but choose fruits opportunistically as they are encountered (Howe and Estabrook 1977; Fleming 1979). The hypothesis is supported by studies such as those of Sorensen (1981), who was unable to find a basis for selection of fruits by British thrushes and titmice, and Worthington (1982, pers. comm.) who concluded that manakins likely take fruits randomly as they are encountered.

The notion that some of these species are specialists on a few fruits while others are indiscriminate generalists on many fruits derives in part from the great abundance and diversity of small, sweet, watery, low quality fruits in comparison to the relatively fewer large, lipid-rich fruits. The apparent richness of the large fruits and their sheer size, which restricts the number of bird species that are able to eat them, offer a plausible basis for assuming that such fruits could provide a staple diet to the few bird species able to eat them and hence allow diet specialization (Snow 1971a; McKey 1975).

However, data on diets of a range of small and large frugivores reveal no particular evidence for marked differences in fruit specialization at the level of the plant family (Table 2). Fruits from only three or four families make up large percentages of the diets of all birds studied.

TABLE 2  
THE THREE OR FOUR DOMINANT PLANT FAMILIES IN THE DIETS OF SOME NEOTROPICAL FRUIT-EATING BIRDS

	Body weight (g)	No. species in diet	% diet comprising 3-4 dominant families	Aquifoliaceae	Araceae	Araliaceae	Bromeliaceae	Burseraceae	Cactaceae	Caprifoliaceae	Chrysobalanaceae	Dilleniaceae	Euphorbiaceae	Flacourtiaceae	Guttiferae	Lauraceae	Loranthaceae	Malvaceae	Melastomataceae	Meliaceae	Moraceae	Palmae	Rubiaceae	Sapindaceae	Solanaceae	Theaceae	Ulmaceae	Sources <sup>1</sup>
<i>Pipra erythrocephala</i>	13.0	43	79		X								X														2	
<i>P. mentalis</i>	14.4	29	65																								4	
<i>Manacus manacus</i>	17.0	66	61																								3	
<i>M. vitellinus</i>	17.6	38	59		X																						4	
<i>Chiroxiphia linearis</i>	21	37	51					X																			5	
<i>Cyanerpes caeruleus</i>	12.6	12	70																								1	
<i>Dacnis cayana</i>	14.1	26	89		X																						1	
<i>Cyanerpes cyaneus</i>	14.2	12	68																								1	
<i>Euphonia violacea</i>	14.7	19	62				X																				1	
<i>Chlorophanes spiza</i>	18.2	14	78																								1	
<i>Tangara guttata</i>	18.4	14	89																								1	
<i>T. gyrola</i>	20.7	32	76																								1	
<i>T. mexicana</i>	20.9	26	62	X																							1	
<i>Ramphocelus carbo</i>	28.5	39	79			X																					1	
<i>Tachyphonus rufus</i>	36.2	31	68																								1	
<i>Thraupis episcopus</i>	37.1	23	61																								1	
<i>T. palmarum</i>	38.6	24	68																								1	
<i>Turdus plebejus</i>	95	44	50 <sup>2</sup>																								5	
<i>Aulacorhynchus prasinus</i>	162	96	70 <sup>2</sup>																								5	
<i>Querula purpurata</i>	100	8 <sup>3</sup>	90																								6	
<i>Procnias averano</i>	120	41 <sup>3</sup>	62					X																			7	
<i>Rupicola rupicola</i>	140	26 <sup>3</sup>	74		X		X																				8	
<i>Procnias tricarunculata</i>	210	29	82			X		X																			5	
<i>Perissocephalus tricolor</i>	340	37 <sup>3</sup>	82																								9	
<i>Pharomachrus mocinno</i>	206	43	99																	X							5	
<i>Steatornis caripensis</i>	415	37	99				X													X							10	

<sup>1</sup> Sources: 1 = Snow and Snow 1971; 2 = Snow 1962b; 3 = Snow 1962a; 4 = Worthington 1982; 5 = Wheelwright et al. 1984, Wheelwright, pers. comm.; 6 = Snow 1971b; 7 = Snow 1970; 8 = Snow 1971c; 9 = Snow 1972; 10 = Snow 1962c.

<sup>2</sup> Estimates only (N. T. Wheelwright, pers. comm.).

<sup>3</sup> Species recorded during breeding season only.

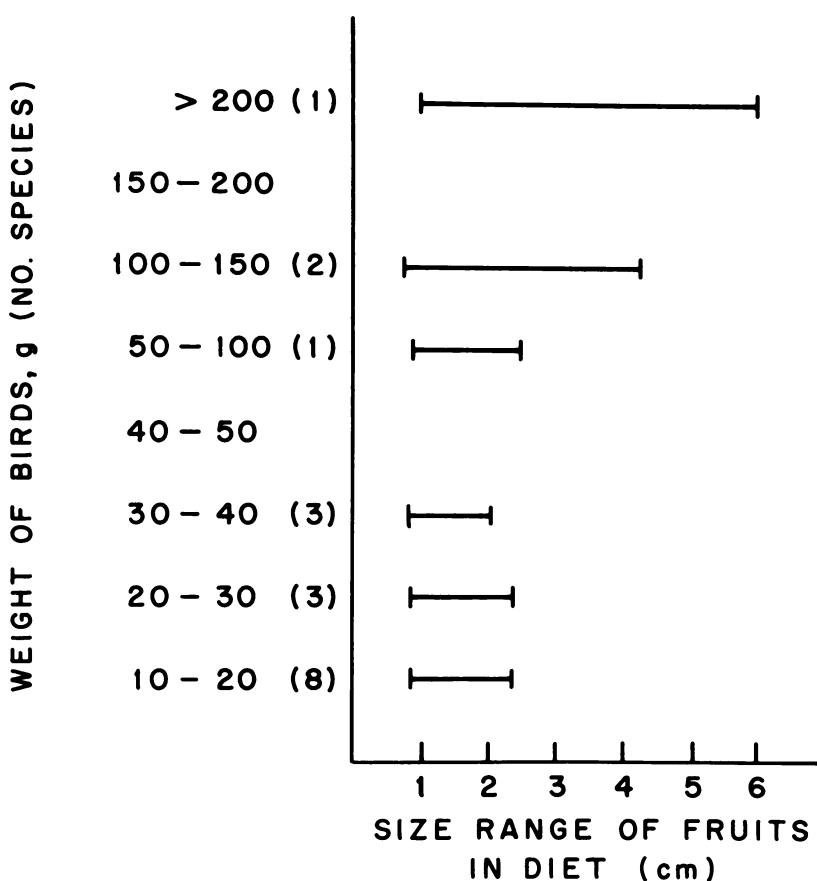


FIG. 1. Fruit sizes in the diets of neotropical frugivorous birds grouped according to body weight. Data summarized from sources listed in Table 2.

Although some large frugivores are closely dependent on a few species of fruiting trees, most take a diversity of fruits and concentrate on three or four plant families.

Even dependence at the family level is not rigid, as can be seen by comparing the diets of two congeneric pairs of manakins (considered specialists by Snow 1981). *Pipra mentalis* and *P. erythrocephala* are morphologically and ecologically very similar, and *Manacus manacus* and *M. vitellinus* are so similar that Snow (1979) described them as subspecies of *M. manacus*. On the large island of Trinidad, berries of the diverse family Melastomataceae figure prominently in the diets of both species (*P. erythrocephala*—63 percent of fruits eaten; *M. manacus*—47 percent, Snow 1962a, b). On the very small Orchid Island, melastomes are much less diverse and apparently less common (Worthington 1982). In any case they are not particularly important to the two manakins there, both of which, however, include a high proportion of fruits of epiphytes in the family Araceae in their diets (*P. mentalis*—22 percent, *M. vitellinus*—18 percent).

Small birds are restricted in the diameters of fruits they are able to swallow by the size of their gapes. Data on the sizes of fruits in the diets of large birds shows that they take both large and small fruits, including the small fruits taken by small species (Fig. 1; Wheelwright, in press). Although a number of large species do feed extensively on the large fruits of lauraceous plants (Snow 1981), many of these take a variety of other fruits (Table 2; Wheelwright 1983; Wheelwright et al. 1984). Even when we consider cases where the degree of dependence between the bird and plant is assumed to be very strong, as with mistletoes and their dispersers (e.g., *Dicaeum* spp., Docters Van Leeuwen 1954; Salomonsen 1964; Euphonias, Snow 1981; *Phainopepla*, Walsberg 1975; *Zimmerius* (*Tyranniscus*), G. Stiles, pers. comm.; pers. observ.;

*Ampelion (Zaratornis) stresemanni*, Parker 1981), we find that the bird species span a wide range of size and families and that none of the birds feeds exclusively on the mistletoe berries.

With respect to the fruits for which data are available, both tanagers and manakins feed mainly on small, juicy fruits that are rich in carbohydrate but relatively low in lipid (Tables 1, 2). Larger birds (5 species of cotingas, a trogon, the Oilbird, and a toucanet) include both lipid rich and carbohydrate rich fruits in their diets (Tables 1, 2). But, with the exception of the Oilbird, median protein contents of fruits in families in the diets of frugivores were not different from the median for all fruits analyzed.

Also, no evidence suggests that highly frugivorous birds provide higher quality dispersal or that plants and their dispersers are tightly co-evolved (Wheelwright and Orians 1982). The same tree species is likely to be visited by different frugivores in different parts of its range (Howe and Primak 1975; Howe 1977), and frugivores may exploit different plant families in different parts of their ranges (Snow 1962a, b; Worthington 1982).

With regard to the selectivity of fruit-eating birds, experimental work with caged birds indicates strong feeding preferences among a wide variety of fruit-eating birds. Although all of the bases for these choices are not yet known, some patterns are becoming clear. Costa Rican tanagers, saltators, and manakins each show hierarchical preferences among fruits of different species, ripeness, size, and accessibility (Moermond and Denslow 1983). Preference for fruits with large pulp/seed ratios have been demonstrated for toucans (Howe and Vande Kerckhove 1980), *Sylvia atricapilla* (Herrera 1981), and aracaris and trogons (Santana C., Moermond, and Denslow, unpubl. data).

Responses of the birds to particular characteristics of the fruits themselves are not too surprising, but experimental aviary and field studies have also shown that the accessibility of fruits strongly influences fruit choice (Denslow and Moermond 1982, in press; Moermond and Denslow 1983). Numerous observations of responses of birds in the field to fruits differing in accessibility (e.g., D. W. Snow 1971b; Snow and Snow 1971; Howe 1977; B. K. Snow 1977; Simms 1978; Kantak 1979; Sorensen 1981; Denslow and Moermond 1982, in press) underscore the likely importance of this aspect of fruit selection. This may be particularly critical with regard to adaptations for frugivory, since it is the single characteristic of fruits most likely to influence the morphology of the bird.

## BEHAVIOR AND MORPHOLOGY

### METHODS OF HANDLING FRUIT

Fruits may be swallowed whole, eaten piecemeal, or mashed. Many birds actively handled fruits in their bills, rotating or moving the fruit with rapid movements of the mandibles. We refer to this action as mandibulation to distinguish this action on the item from the effect on the item (cf. Kear 1962; Snow and Snow 1971; Moermond 1983). Cases in which a fruit is mandibulated to such an extent that it is partially flattened or crushed we have termed "mashing" (Moermond 1983). When fruits are swallowed whole, the amount of mandibulation is usually minimal. Eating fruits in piecemeal fashion refers to cases in which birds bite or tear our chunks of pulp. These differences in fruit handling are potentially of great importance to the plants and are likely to have differing consequences to the birds' feeding and digestion rates.

The size of fruit swallowed by a bird is limited by the breadth of its gape, where fruit is defined as the unit of seed(s) and surrounding pulp that is ingested (Snow 1973; Wheelwright, in press). Small birds such as *Manacus* spp. can only handle fruits smaller than about 15 mm diameter; seeds of large fruits, such as those of many Lauraceae and Palmae, can be dispersed only by birds that have large gapes such as the larger cotingas and a number of the non-passeriform frugivores. Many fruits, however, consist of removable units containing one or a few seeds with the surrounding pulp within a woody capsule (e.g., *Guarea* spp., Meliaceae; *Glusia* spp., Guttiferae). As with berries and drupes, the frugivore is limited by the diameter of the unit to be swallowed. Seeds may be either defecated if small or regurgitated if large (Snow 1971a; Worthington 1982; Moermond and Denslow, unpubl. data). In both cases the seed is carried within the bird from several minutes to an hour or more before being dropped (pers. observ.; D. J. Levey, pers. comm.).

Mashing of fruits appears to be nearly completely restricted to the tanagers and emberizid finches (Moermond 1983). Other birds, such as manakins, certainly mandibulate their fruits to some extent, but such actions appear to serve primarily for positioning the fruit in prep-

aration for swallowing and only on rare occasion is the fruit actually crushed (Moermond and Denslow, unpubl. data). All 20 species of tanagers we have observed crush the fruit pulp, often thoroughly, squeezing out and swallowing much of the fruit pulp and juice. In the case of very small fruits (<3 mm diameter), the mashing may be very rapid (<1 sec), and Snow and Snow (1971) reported that some species of *Tangara* swallow small fruits whole without noticeable mandibulation. Moermond (1983) has suggested that the "suction-drinking" capability of tanagers may be directly related to efficient swallowing of juice crushed out of watery fruits. In addition, large seeds, as well as the tough outer skin of some fruits, are frequently separated from the pulp and dropped during the mashing process. This reduces the bulk of indigestible material to be processed but also results in little dispersal of the seeds of fruits with even moderately large seeds (>3.5 mm diam., Moermond and Denslow, unpubl. data). Whether or not a seed is dropped depends not only on the size of the seed and the size of the bill but also on the bill shape and the handling technique of the bird. This was recently demonstrated in systematic experiments with captive birds of five tanager species and four other frugivorous species in Costa Rica (D. J. Levey, unpubl. data).

Small seeds, such as those found in *Phytolacca* (Phytolaccaceae), many *Psychotria*, and *Melastomataceae*, are usually swallowed whole by tanagers along with the crushed pulp and the juices. In some epiphytic plant species with small fruits, small seeds, and a tough fruit coat such as *Rhipsalis* (Cactaceae) and many species of *Anthurium* (Araceae), the fruit coat is nearly always dropped by tanagers, but the seeds are forced out of the fruit with the first drops of pulp and juice as the fruits are mashed and all are swallowed together before the seed coat is dropped (Moermond and Denslow, unpubl. data). This is likely an adaptation of the plant to insure ingestion of the seeds by fruit mashers such as *Euphonia* tanagers that are often the principal consumers of these fruits.

Eating fruits piecemeal is not the speciality of any particular species of frugivore but rather appears to be a facultative response to fruits that are large relative to the bird's gape. Birds that have strong bills such as toucans, barbets, tanagers, and finches are the most likely to eat piecemeal fruits too large to be easily swallowed whole (Snow and Snow 1971; Skutch 1981; pers. observ.); however, even relatively weak-billed birds such as the manakins occasionally eat pieces out of large soft fruits such as those of *Coussarea* (Rubiaceae; pers. observ.; D. J. Levey, pers. comm.) and *Henriettea* (Melastomataceae; Snow 1962b) or out of catkins or compound fruits (Snow 1962a). The ability of birds to eat fruits piecemeal increases the size range of exploitable fruits beyond those that are swallowed whole.

The fate of seeds from fruits eaten piecemeal depends on how and where they are eaten. Large cultivated fruits such as papaya (*Carica papaya*), banana (*Musa sapiens*), and the Pejiballe palm (*Bactris gasipaes*) are regularly eaten in piecemeal fashion. Pejiballe fruits attract many species of birds and mammals, but among the birds, only a few very large species, such as oropendolas (*Gymnostinops montezuma*), are actually able to carry the intact fruit from the tree (pers. observ.). Other fruits, such as *Cecropia* (Moraceae), *Clusia*, *Drymonia* (Gesneriaceae), *Piper* (Piperaceae), *Stemmadenia* (Apocynaceae), and *Xylopia* (Annonaceae), appear to be adapted to being eaten piecemeal in that the seeds are small and imbedded in the matrix of pulp which is eaten.

In other cases fruits eaten piecemeal are first carried away from the plant, and the seeds thus dispersed to some degree, e.g., *Tersina viridis* eating large fruits (Schaefer 1953), *Trogon massena* eating large lauraceous fruits in captivity (Santana C., Moermond, and Denslow, unpubl. data), *Ramphastos sulfuratus* and *Pteroglossus torquatus* eating *Swartzia cubensis* fruits, and *Euphonia gouldi* eating *Asterogyne martiana* fruits (pers. observ.). Whether or not the seeds of fruits eaten piecemeal are dispersed effectively bears on the coevolution between the plants and their dispersers and hence may influence the nature of food resources available to fruit-eating birds.

#### BILL MORPHOLOGY

Given the diverse set of species that regularly take fruits, the absence of common morphological adaptations for fruit-eating *per se* is not surprising (see Karr and James 1975; Ricklefs 1977). Even bills, the structures used directly for "capturing" and handling fruits, exhibit no common pattern, as can be seen in part by examining the diversity of bill shapes among tanagers (Storer 1969) and frugivorous tyrannids (Traylor and Fitzpatrick 1982). Nevertheless, if differences in the methods of taking and handling fruits are considered, a few general adaptive features of bill size and shape can be seen. A statistical comparison of a large set of temperate

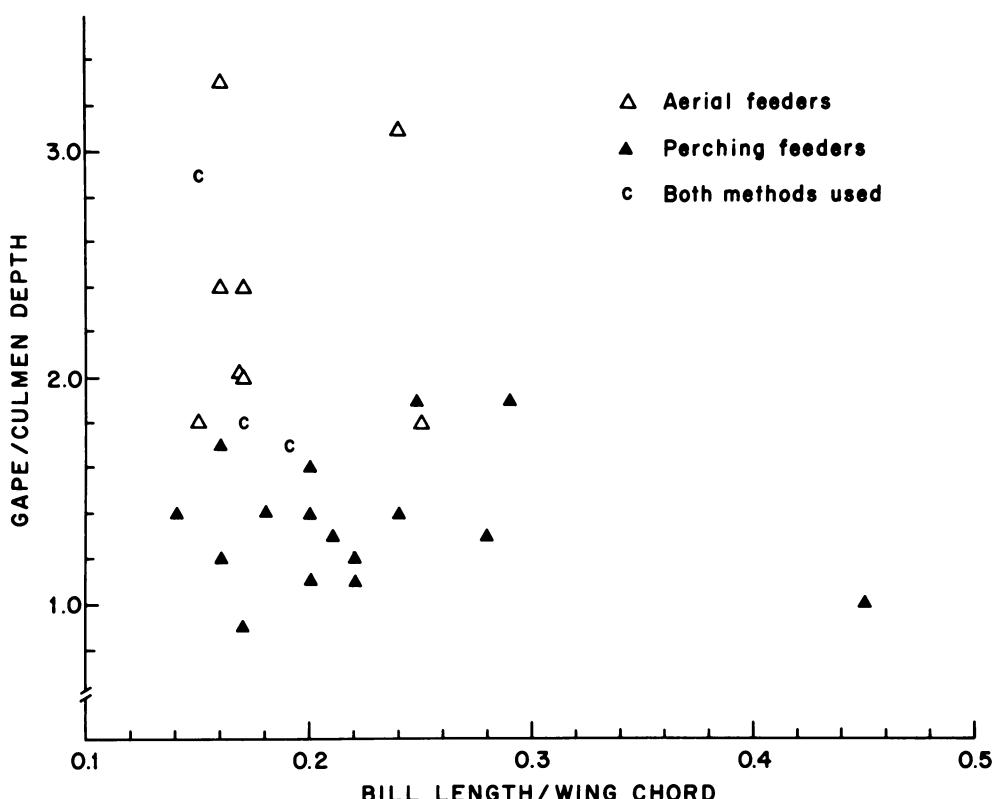


FIG. 2. Variation in bill size and shape associated with different methods of removing fruits. Gape/ culmen depth is used to separate wide flat bills from narrow deep ones. Measurements are from skins in the University of Wisconsin Zoology Museum representing 28 species in 11 families or subfamilies of neotropical frugivorous birds. Culmen depth was taken at the base of the nares and bill length from the juncture with the skull.

species feeding on fruits in southern Spain demonstrated that those species (all muscicapids) that were actual seed dispersers (swallowing fruit whole) had flatter and wider bills than species that were seed and pulp predators (Herrera 1984). We compared bill shape to method of capturing fruits by plotting the ratio of gape width to culmen depth against relative bill size (bill length/wing chord) for a diverse set of species (Fig. 2). Species that predominantly use flight to take fruits have relatively short, wide, flat bills which separate them sharply from those picking or reaching fruit while perched. A similar pattern appears also among insect-eaters (Partridge 1976).

Frugivores from several families that have relatively wide, flat bills commonly take fruits on the wing (see next section). Even within families in which most species predominantly take fruits from perches, those species that take many fruits on the wing again have the widest, flattest bills, e.g., *Tersina viridis* (Thraupinae) and *Myadestes melanops* (Turdinae).

Although a wide bill is in part associated with aerial feeding *per se*, a wide bill and gape are also advantageous for handling and swallowing large fruits. Among African drongos (Dicruridae), a family of birds that take most of their food items on the wing, the species that are most heavily frugivorous have shorter, flatter bills (Karr and James 1975). Similarly, among the flycatchers, many of which take their food on the wing, some of the most heavily frugivorous species (e.g., *Myiozetetes* spp., *Megarhynchus pitangua*, *Myiodynastes* spp., *Legatus leucophaius*) have wider and flatter bills than average (Traylor and Fitzpatrick 1982). Other highly frugivorous flycatchers such as *Mionectes* spp., *Elaenia* spp., and *Zimmerius* (*Tyranniscus*) spp., that feed on relatively small fruits, have short, somewhat terete bills, but nevertheless still have relatively large gapes (F. G. Stiles, pers. comm.). A parallel pattern is

found among cotingas, most of which are highly frugivorous and take most food on the wing. Those species such as *Procnias* and *Xipholena* that feed on relatively large fruits have very wide and short bills, whereas those species such as *Capornis* and *Pipreola* that eat relatively small fruits have short but narrower and less specialized bills (Snow 1982). The Sharpbill, *Oxyruncus cristatus* (recently placed in the Cotingidae, Sibley et al. 1984) which has a longer, narrower bill than most cotingas, takes fruits by reaching and hanging (F. G. Stiles, pers. comm.).

The advantage to a frugivore of a large gape is clear since gape size limits the size of fruit that can be swallowed (Snow 1973; Wheelwright, in press), but the bill length and strength may be associated with other aspects of fruit handling. Virtually all the aerial feeders we considered (Fig. 2) swallow fruits whole; however, the type of fruit handling employed by species with longer, deeper bills appears to depend on the presence of other structural features of the bills. For example, although wide bills need not also be long, a long bill may be advantageous for reaching fruits from perches. Woodpeckers, barbets, and toucans, which often swallow fruits whole, have long to extremely long, deep bills, which they use to reach fruits from perches. The toucans, in particular, reach much farther with their long bills than any other frugivore and are so dexterous that they are able to select and pick individual small fruits with the tip of the bill (Santana C., Moermond, and Denslow, unpubl. data).

Tanagers and finches, which also pick most of their fruits from perches, mash most of their fruits. These birds have short to relatively long beaks that are markedly narrower, deeper, and frequently much stronger than those of aerial fruit-eaters. Their bills have well-developed lateral ridges on the horny palate (Beecher 1951), which may facilitate ingestion of crushed pulp and juice as they mash fruits. Some species, such as the *Ramphocelus* tanagers, have expanded ramphothecae, which may act to prevent fruit juices from fouling the feathers (Storer 1969).

Within each of the groups discussed, modifications in bill shape and form may influence the method of fruit handling and the types of fruits taken. Although few appropriate data exist, two within-family comparisons will serve to illustrate consequences of relatively minor differences in bill shape. Within the Trogonidae, both *Trogon massena* and *Pharomachrus mocinno* are highly frugivorous, and both frequently eat large lauraceous fruits (Skutch 1972; Wheelwright 1983). Differences in bill size and strength, however, affect the ways in which the two species handle fruits. The bill of *T. massena* is narrower, deeper, relatively longer, and noticeably heavier than that of *Pharomachrus* (Fig. 3), even though *T. massena* is markedly smaller than the *P. mocinno* (141 g vs 206 g). In captivity, *T. massena* has been observed to eat large lauraceous fruits piecemeal (Santana C., Moermond, and Denslow, unpubl. data), whereas in a detailed field study Wheelwright never observed *P. mocinno* to eat fruits piecemeal (N. T. Wheelwright, pers. comm.). Similarly, among paleotropic fruit-eating pigeons, the strong-billed *Treron* spp. are able to bite chunks out of fruits whereas the weaker billed *Ducula* and *Ptilinopus* spp. swallow fruits whole (Goodwin 1970).

Such examples further reinforce the idea that bill shape and size are likely to influence which fruits can be taken most efficiently. We contend that bill features are more likely to be associated with particular fruit handling behavior than with the frugivorous habit in general.

#### METHODS OF TAKING FRUITS

Snow and Snow (1971) suggested that fruit can be plucked by birds in only a few different ways. We agree, but suggest that differences among those ways influence which fruits are most accessible and the benefit:cost ratio of taking those fruits. Although few quantitative data are available, we shall offer descriptions of techniques birds use to "capture" fruits and, with a few examples, propose how the capture techniques may influence fruit selection. Examination of both fruit capture methods and their morphological correlates (see next section) provides a basis for understanding adaptive divergence and specialization among frugivores.

Fruits may be taken on the wing or from a perched position (Herrera and Jordano 1981; Denslow and Moermond, in press). A comparison of the use frequencies of these two general techniques for 10 bird species feeding on the same tree (Fig. 4) illustrates a typical pattern: most species predominantly use only one of the two techniques, taking fruits either on the wing or from a perch. Only two of the species in this example, the *Tityra* and the *Catharus* thrush, commonly used both techniques. Despite the strong implication of stereotypy in fruit capture techniques among these species, nearly all of them occasionally used the other technique. If other fruit species were included in the comparison, the versatility in foraging

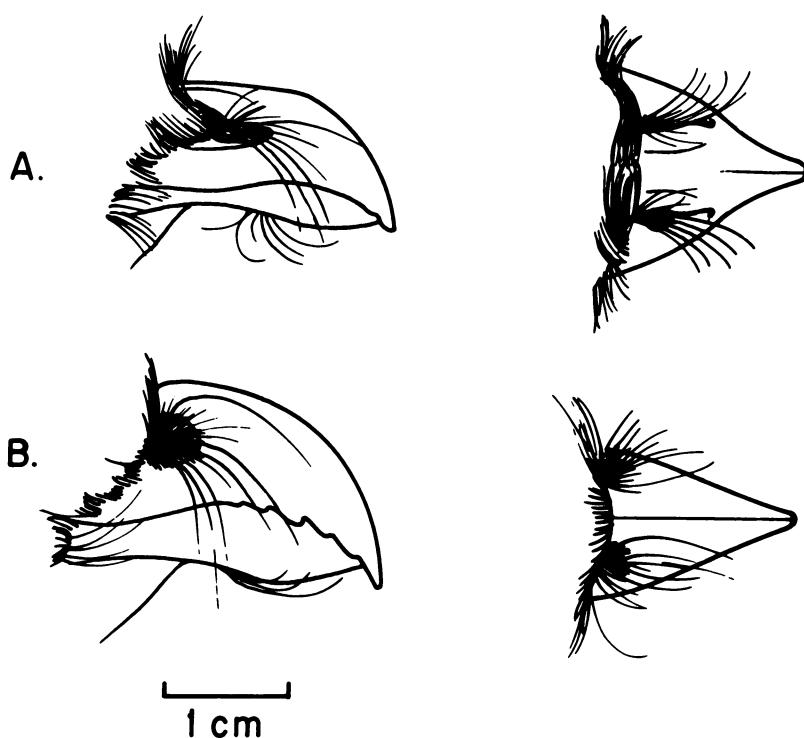


FIG. 3. Bill shapes (lateral [left] and dorsal [right] views) of male (A) *Pharomachrus mocinno* and (B) *Trogon massena*. The bills were drawn from specimens in the University of Wisconsin Zoology Museum.

techniques used by several bird species would be more obvious. For example, even though *Pteroglossus torquatus* rarely takes fruit on the wing, captive *Pteroglossus* were induced to take fruits on the wing repeatedly under exceptional circumstances in which highly desirable food items were inaccessible by any other capture method (Santana C., Moermond, and Denslow, unpubl. data). The *Querula* which clearly took most *Miconia multispicata* fruits on the wing, as is typical for this cotinga, was observed to regularly perch "to pluck the fruits of *Didymopanax morototoni* and *Guarea trichilioides*, both of which bear their fruits in large bunches on strong stalks that afford a foothold" (Snow 1971b:7). *Perissocephalus tricolor* is another larger cotinga that takes most fruits exclusively on the wing, except when feeding on *Didymopanax* fruits which it picks while perched (Snow 1972).

These two fruit capture categories can be further divided to reveal additional functional differences among frugivores. Unfortunately, few studies report fruit capture techniques, and those that do often use general categories that are inconsistent from study to study. The subtle functional differentiation of prey capture methods recently applied to some insect-eaters (Davies and Green 1976; Fitzpatrick 1980) has not yet been developed for fruit-eaters. The following descriptions are based on our own observations of over 80 species of neotropical birds in the field in numerous localities and on experiments with 23 species of six families in captivity.

We have observed four distinct flight maneuvers used to pluck fruit while on the wing: hovering, stalling, swooping, and snatching. A hovering bird pauses in front of the fruit while flapping its wings so as to maintain zero air speed. This method is used commonly by manakins, tyrannid flycatchers, and many small tanagers, especially those that weigh less than 20 g, such as *Tangara* and *Euphonia* spp. A stalling bird pauses briefly in front of the fruit by using a very steep wing attack angle allowing the bird to slow down and stall just in front of or below the fruit. Both hovering and stalling are functionally equivalent to "hover-gleaning" of Fitzpatrick (1980), but the flight motions employed and the morphological features associated

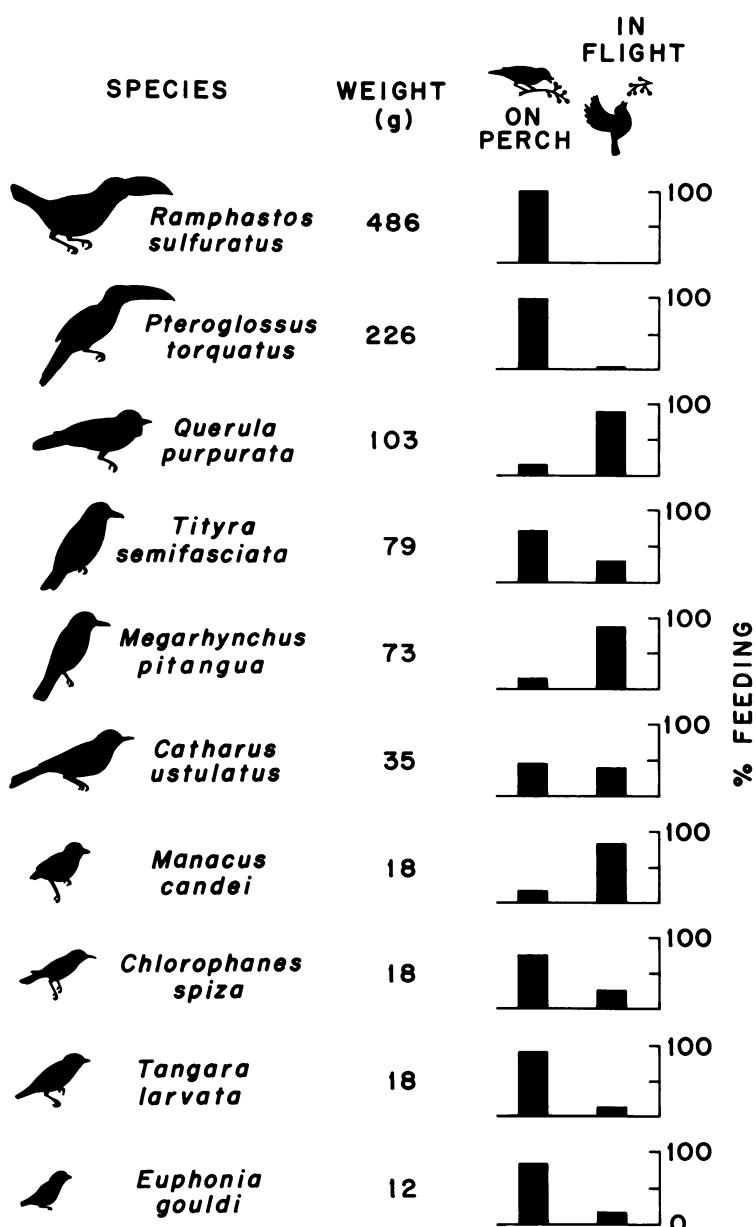


FIG. 4. Feeding behavior of the most common visitors to *Miconia multisepicata* (Melastomataceae). Histograms show percentages of total fruit removals (Denslow and Moermond, in press, with additions).

with each technique differ (see next section). *Trogon massena* was observed and photographed while stalling, and morphological examination of trogon species of three genera (*Trogon*, *Pharomachrus*, and *Harpactes*) suggest this technique may be generally employed by the Trogonidae and possibly *Phoenicircus* spp. (Cotingidae; Moermond and Santana C., unpubl. data). Swooping and snatching both involve continuous movement past the fruit as it is taken. In swooping, the wings are held out and the bird glides up to the fruit, whereas in snatching, the wings are flapped throughout. In both cases, some forward momentum is conserved in

contrast to hovering or stalling in which the bird actually stops at the point of contact with the fruit. We have observed swooping used by several cotingids (*Querula purpurea*, *Carpodectes nitidus*) and by *Tityra* spp. (*Tityrinæ*).

We suspect that nearly all species may at times snatch fruits, but the first three methods are used primarily by those species that use flight to capture most of their food items. The costs and skill of taking fruits by snatching and swooping are likely to differ from those associated with hovering and stalling. Hovering and possibly stalling are likely to be more costly than snatching or swooping (Pennycuick 1975; Rayner 1981), but the total distance flown when capturing a fruit is sometimes shorter for those using hovering vs snatching. Hovering and stalling may allow a more precise approach to fruits that are less accessible from a longer flight. Snatching and swooping may result in more "misses" and possibly more "collisions" with twigs and infructescences.

Birds that take fruits from perches may do so in three different ways, by picking, reaching, or hanging. While birds using all of these techniques "pick" or "reach" fruit in an ordinary sense, we have restricted use of these terms to describe the position assumed by the bird when taking the fruits. "Picking" refers to all cases where the birds take fruits close to their perch without extending their bodies or assuming special positions. "Reaching" refers to cases in which the bird extends its body out or down from the perch. Appropriate qualifiers or adjectives can be applied as necessary to distinguish the degree of reach (e.g., tarsus above or below level of perch, wings fluttered or not, reach horizontal or vertically down). Hanging refers to cases in which the bird's entire body and legs are under the perch with the ventral side up. Picking and reaching are often used by a wide variety of birds, but we have seen only woodpeckers (e.g., *Melanerpes pucherani* and *Campephilus guatemalensis*) regularly hanging below perches when eating fruits.

Although virtually all birds are able to pick fruits close to perches, few are able to reach very far below a perch. Some appear restricted to taking fruits within easy reach of a perch, while others can reach outward or downward close to the limit of their body length (Denslow and Moermond, in press). The ability to use reaching or hanging does not appear to be associated with the ability to take fruits on the wing. Some species that take fruits primarily on the wing, such as trogons, flycatchers, some manakins (e.g., *Manacus*), and some cotingids (e.g., *Querula*, *Cephalopterus*), are unable to reach well from a perch (Snow 1982; Denslow, Moermond, and Santana C., unpubl. data), but other primarily aerial feeders, such as *Tityra* spp., and several cotingids (e.g., *Procnias*, *Carpodectes*) regularly reach fruits from a perch (Snow 1977; Santana C. and Milligan 1984; pers. observ.).

Likewise, birds that take most of their fruits from perches also differ considerably in their ability to reach. Neotropical thrushes (Turdinae) and emberizine ground finches (e.g., *Arremon aurantiirostris* and *Arremonops conirostris*) are poor reachers. These species tend to take all their fruits by either picking or snatching (e.g., *Catharus ustulatus* in Fig. 4). Toucans, barbets, and most tanagers can reach well below perches. The tanagers are particularly interesting in this respect, showing considerable variation in reaching ability among similar-sized species. Some tanagers such as *Thraupis palmarum* (36 g) and *Euphonia gouldi* (12 g) are so adept at reaching that they can extend their entire bodies and legs below the perch and recover their original upright position without the aid of their wings (Denslow and Moermond, unpubl. data). Others such as *Habia fuscicauda* and *Ramphocelus passerinii* are relatively poor reachers as tested in aviary experiments (Denslow and Moermond, in press, unpubl. data; D. J. Levey, pers. comm.).

Differences in reaching ability observed in the field were described for tanagers and honeycreepers of Trinidad by Snow and Snow (1971). Their descriptions correspond to our observations on Costa Rican species and show that marked differences in such abilities may be found within the same genus. For example, *Thraupis palmarum* and *Tachyphonus delatrii* demonstrated greater reaching abilities than *Thraupis episcopus* and *Tachyphonus rufus*, respectively. Although such abilities have been little studied, they seem to be associated with some readily identifiable morphological traits (see next section) and, as with different flight techniques, they also likely influence the types of fruits that can be efficiently exploited.

We compared the limits of reach of two small tanagers to that of *Manacus candei* (Fig. 5). All three species were able to pick fruits above them at nearly full body lengths, but only the tanagers were able to reach full body lengths downward. Similar determinations of the distances fruits can be taken from a perch for *Pteroglossus torquatus* and *Trogon massena* demonstrated a similar pattern. *Pteroglossus* was able to reach a full body length below its perch, whereas

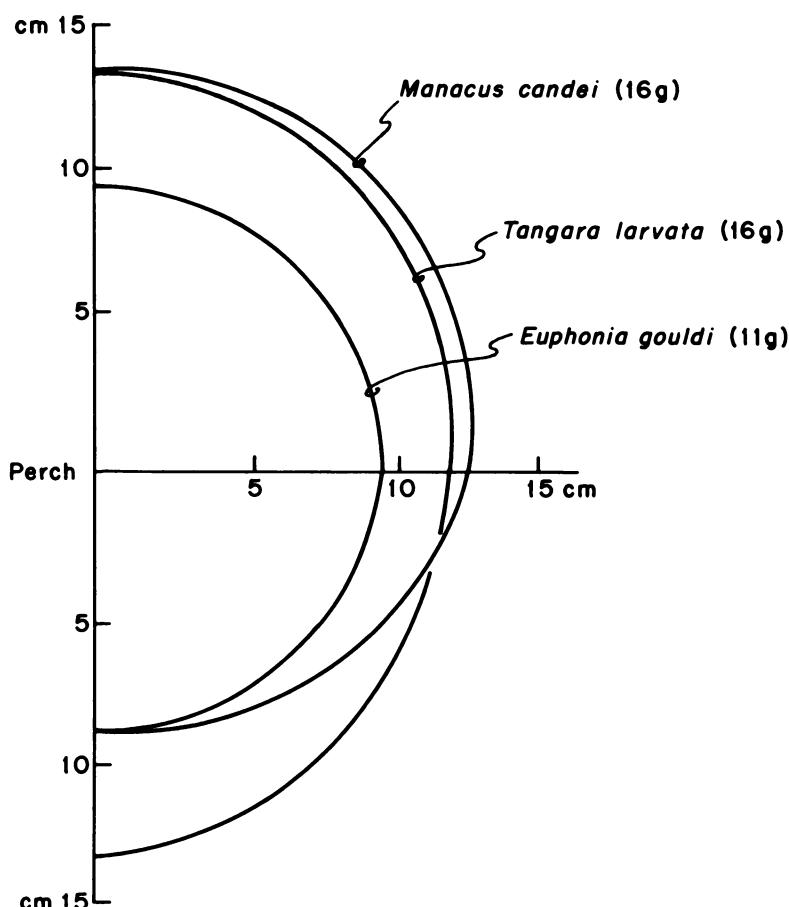


FIG. 5. Distances of maximum reach in 3 directions from a sturdy perch for 3 small frugivores. *Manacus candei*, an aerial feeder, can reach only as far below the perch as the much smaller *Euphonia gouldi*, a perching feeder.

the trogon was able to pick fruits slightly below the perch only with difficulty and was unable to reach (Santana C., Moermond, and Denslow, unpubl. data). Clearly such differences are likely to restrict the number of fruits that can be taken by the manakin or trogon from a single perch relative to the number obtainable by the tanagers and toucanet. On the other hand, both the manakin and the trogon were adept at taking fruits on the wing and in aviary experiments were shown to select fruits hanging clear from perches (Denslow, Moermond, and Santana C., unpubl. data). In the field both species commonly take hanging fruits that other species take only rarely and with difficulty.

Species using different fruit capture techniques can exploit the same species of fruit (Fig. 4); however, detailed data are likely to show that species using different techniques take fruits from different portions of the tree as has been reported in other studies (Kantak 1979; Herrera and Jordano 1981; Santana C. and Milligan 1984). All fruits in a tree were not equivalent resources contrary to such a suggestion by Leck (1971b); fruits on an infructescence differ with respect to distances to a perch and thus to accessibility and cost of "capture" to different species of birds. Differences in feeding techniques and ability therefore may affect which fruit species are incorporated into a bird's diet.

A comparison of trogons, which rarely take fruits from a perch, to toucans which are rarely observed to take fruits on the wing (Wagner 1944; Skutch 1971, 1972; Bourne 1974; Wheelwright 1983; Santana C. and Milligan 1984), illustrates other possible consequences of

differences in feeding technique. Trogons usually take only one fruit per sally whereas toucans frequently reach and take multiple fruits from one perching position. We suggest that the likely greater expenditure per fruit by the trogon leads it to use a narrower range of fruit types compared to toucans. In aviary experiments *Trogon massena* showed a nearly exclusive preference for fully ripe *Hamelia patens* (Rubiaceae) fruit; whereas *Pteroglossus torquatus* readily accepted several stages of less than fully ripe *Hamelia*, although fully ripe fruits were their first choice (Santana C., Moermond, and Denslow, unpubl. data). As a consequence, trogons are also expected to include fewer fruit species in their diets than toucans as has been shown for *Pharomachrus mocinno* (43 spp.) vs *Aulocorhynchus prasinus* (96 spp.; Wheelwright 1983).

When additional appropriate species pairs are studied in sufficient detail, these comparisons may be extended. Our own fruit selection experiments with manakins (aerial fruit feeders) and tanagers (primarily perching fruit feeders) suggested that manakins were more discriminating in choices between paired fruits of different fruit species than were tanagers (Moermond and Denslow 1983), and recently completed experiments by Levey show that manakins accept fewer stages of ripening berries (i.e., only those fully ripe or nearly fully ripe) than do tanagers and that the manakins are more precise in their selection among sets of fruits at different stages of ripeness (D. J. Levey, pers. comm.).

These differences in fruit selection are likely based on differences in the benefit : cost ratio associated with each technique of fruit capture. Differences in the costs depend not only on the technique used but also on the ability of each bird species to execute the maneuvers required to use the technique. Such abilities will be determined in large part by morphology.

#### LOCOMOTORY MORPHOLOGY

Morphology is assumed to determine the diversity of the food capture techniques employed by a given bird species, their relative costs, and the efficiencies with which they are used.

**Wings.**—Basic aerodynamic principles dictate that the size of bird and the size and shape of its wings strongly influence flight characteristics and options (e.g., Savile 1957; Pennycuick 1969, 1975; Kokshaysky 1973; Greenewalt 1975; Rayner 1981). A few general predictions can be made with regard to wing length, wing loading, and degree of slotting. For a bird of a given weight, long wings reduce the costs of flight (Pennycuick 1969, 1975; Hails 1979) and aid hovering (Norberg 1979), whereas short wings increase stability and maneuverability (Savile 1957; Kokshaysky 1973; Norberg 1981), increase acceleration due in part as a result of higher wing beat frequency (Kokshaysky 1973; Norberg 1981), and reduce the inertial forces on the wing skeleton (Norberg 1979, 1981). Low wing loading reduces the cost of flight (Pennycuick 1969, 1975; Greenewalt 1975) and, as a consequence, aids hovering and maneuverability (Norberg 1981). Increased slotting of the primaries allows a higher angle of attack of the wing which may increase lift, delay stalling, and increase acceleration (Savile 1957; Brown 1963; Alexander 1968; Kokshaysky 1973). The suggestion that slotting primarily serves to reduce the vortex at the wing tip (Savile 1957; Cone 1968) is not supported (Kokshaysky 1973). All of these predictions are constrained by body weight of the bird. Among geometrically similarly shaped birds, a decrease in size is associated with increases in the margin between power required for flight and the power available (Pennycuick 1969, 1975; Greenewalt 1975) and improvements in most aspects of aerial performance such as rate of acceleration, velocity range, and maneuverability (Norberg 1981; DeJong 1983).

Constraints on flight appear far less critical for birds below about 100 g body weight (Greenewalt 1975; DeJong 1983). Among frugivorous birds heavier than 100 g (Table 3), birds with wing loadings greater than 0.42 g/cm take fruits primarily by reaching, whereas those with lower wing loadings take fruits primarily on the wing. Such a correlation does not hold well for species weighing less than 100 g. Among these forms, some birds that reach well also appear able to hover easily (e.g., several *Tangara* spp. [Denslow and Moermond unpubl. data]), whereas *Manacus* spp., which take virtually all fruits on the wing, have unusually high wing loadings (Table 3, Fig. 6).

Fitzpatrick (1978) showed that large, aerial-feeding tyrannid flycatchers have long and often somewhat slotted wings, while small forest flycatchers have short, rounded wings presumably giving them greater maneuverability. A similar pattern holds for large sally-gleaning antshrikes versus perch-gleaning antshrikes (Schulenberg 1983). However, small frugivores, such as tanagers (*Euphonia* and *Tangara* spp.) and honeycreepers (*Cyanerpes*, *Dacnis*, and *Chlorophanes* spp.) generally have relatively longer and narrower wings ( $\bar{X}$  aspect ratio of 15 species = 1.76)

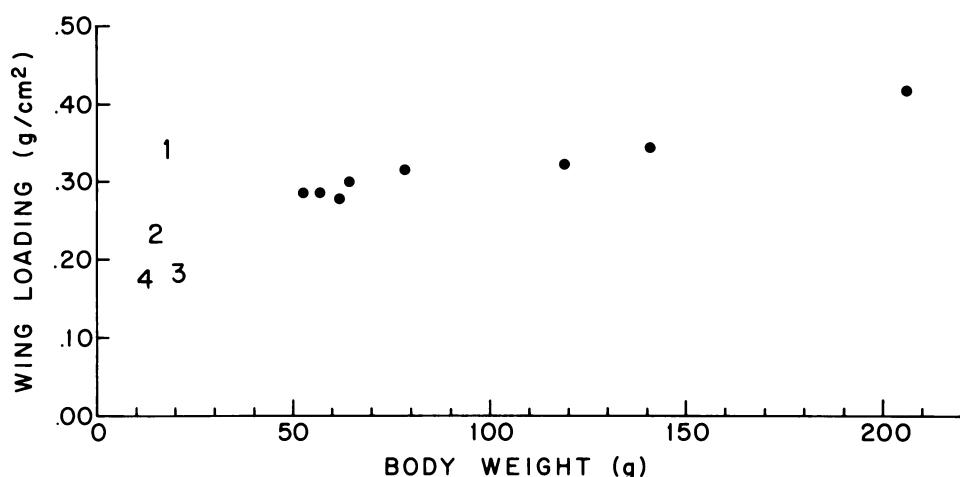


FIG. 6. Wing loading for manakins (numbers) and trogons (closed symbols) of different body weights (data from Hartman 1961); 1 = *Manacus vitellinus*, 2 = *Pipra mentalis*, 3 = *Chiroxiphia lanceolata*, 4 = *Corapipo leucorrhoa*.

than small insectivorous tyrannids (19 species,  $\bar{X} = 1.62$ ) and formicariids (15 species,  $\bar{X} = 1.46$ ) ( $P < 0.01$ , median test; data from Hartman 1961). The short, rounded wings of the insectivores may be important in maneuverability and rapid acceleration in capturing insects. For the tanagers feeding on fruits, the longer wings may enhance their ability to hover for fruits and reduce the flight costs of commuting between fruiting plants. A consequence of longer, narrower wings may be the higher wing loadings of the tanagers compared to similarly sized tyrannids (.16 g/cm vs .22 g/cm;  $P < 0.01$ , median test; data from Hartman 1961).

This first order approach gives an unexpected result when applied to frugivorous manakins which take nearly all their food on the wing. The four manakin species we considered (Table 3) have wings with a mean aspect ratio (1.62) similar to that of the small flycatchers discussed above and distinctly lower than the small tanagers, but manakin wing loadings ( $\bar{X} = .22$  g/cm) are higher than that of the flycatchers but equivalent to that of the tanagers. The functional advantage of this type of wing for the manakins is not clear.

Assessments based on single factors such as wing loading or aspect ratio are unlikely to explain satisfactorily foraging differences among similar species (e.g., Partridge 1976, Levey et al. 1984). Wing loading is highly correlated with body weight for some homogeneous groups of birds such as trogons (8 species in 2 genera), but no clear relationship emerges from a similar plot for four species of manakins of four genera (Fig. 6). Similarly, wing length with respect to body weight varies considerably among tyrannids (Fitzpatrick 1978) and cotingids (Snow 1982), although, in general, larger birds have longer wings. A suite of wing characteristics must be considered to understand differences in foraging style among ecologically similar species (Norberg 1979).

A more detailed comparison of the four species of manakins (Fig. 6) reveals distinct differences in aspect ratio and degree of slotting. *Manacus vitellinus*, with the highest wing loading, has a relatively low aspect ratio and a high degree of slotting, which may compensate for the low wing area. *Pipra mentalis*, with intermediate wing loading, has the highest aspect ratio and virtually no slotting similar to the wings of some *Tangara* tanagers with similar wing loadings. *Chiroxiphia lanceolata* has an intermediate wing loading, relatively low aspect ratio, and an intermediate degree of slotting with fewer and shallower slots than *Manacus*. A similar pattern can be found within the Cotingidae. The Purple-throated Fruit-crow (*Querula purpurata*), (91–112 g) in the Guianas has much longer wings (165–195 mm chord) than the similar-sized Guianan Red Cotinga (*Phoenicircus carnifex*, 75–85 g, 90–110 mm wing chord; Snow 1982). Like *Manacus vitellinus*, *Phoenicircus* has highly slotted wings as compared to the little slotted wings of the fruitcrow (Fig. 7). Regardless of the effect of wing characteristics on courtship displays of these birds, wing morphology should strongly influence feeding behavior. Such parallel patterns in wing loading, slotting, and aspect ratios among divergent

**TABLE 3**  
**MORPHOLOGICAL<sup>1</sup> AND BEHAVIORAL CHARACTERISTICS OF SELECTED SPECIES OF NEOTROPICAL  
 FRUIT-EATING BIRDS**

	Body weight (g)	Flight muscles (% body weight)	Leg muscles (% body weight)	Wing loading (g/cm <sup>2</sup> )	Aspect ratio (span/chord)	FCM <sup>3</sup>	FHM <sup>4</sup>
<b>Columbidae</b>							
<i>Columba speciosa</i>	259	29.1	5.0	0.64	2.0	P	Pr
<i>C. nigrirostris</i>	144	28.7	7.0	0.46	1.8	P	Pr
<b>Psittacidae</b>							
<i>Amazona autumnalis</i>	416	18.7	8.0	0.60	2.0	P	Pr
<i>Pionis senilis</i>	213	20.8	7.2	0.46	2.2	P	Pr
<b>Steatornithidae</b>							
<i>Steatornis caripensis</i> <sup>2</sup>	415	15.6	—	0.29	3.2	A	S
<b>Trogonidae</b>							
<i>Pharomachrus mocinno</i>	206	22.2	3.4	0.42	1.9	A	S
<i>Trogon massena</i>	141	21.8	3.2	0.34	2.0	A	S
<i>T. curucui</i>	50	22.3	2.7	0.28	2.1	A	S
<b>Momotidae</b>							
<i>Momotus momotus</i>	133	20.5	6.2	0.34	1.7	A	S
<b>Capitonidae</b>							
<i>Eubucco bourcierii</i>	33	13.1	9.4	0.33	1.6	P	S
<b>Ramphastidae</b>							
<i>Aulacorhynchus prasinus</i>	155	144	11.0	0.53	1.7	P	S
<i>Pteroglossus torquatus</i>	226	13	9.9	0.52	1.7	P	S
<i>Ramphastos swainsonii</i>	480	14.2	13.0	0.56	1.6	P	S
<b>Picidae</b>							
<i>Phloeoceastes guatemalensis</i>	240	15.3	11.5	0.41	1.7	P	S
<i>Melanerpes pucherani</i>	54	17.9	7.1	0.28	2.0	P	S
<b>Pipidae</b>							
<i>Pipra mentalis</i>	15	19.9	5.4	0.23	1.7	A	S
<i>Chiroxiphia lanceolata</i>	20	18.4	6.5	0.18	1.6	A	S
<i>Corapipo leucorrhoa</i>	12	19.2	5.2	0.18	1.6	A	S
<i>Manacus vitellinus</i>	18	17.8	10.2	0.34	1.6	A	S
<b>Cotingidae</b>							
<i>Cotinga ridgwayi</i>	57	25.2	6.4	0.31	1.9	A/P	S
<i>Lipaugus unirufus</i>	80	21.1	—	0.29	1.9	A	S
<i>Querula purpurata</i>	103	17.1	5.0	0.15	1.7	A	S
<b>Tyrannidae</b>							
<i>Tityra semifasciata</i>	79	18.4	9.2	0.33	1.7	A/P	S
<i>Tyrannus melancholicus</i>	40	24.4	3.4	0.21	1.9	A	S
<i>Legatus leucophaius</i>	26	22.1	4.3	0.22	2.0	A	S
<i>Myiodynastes maculatus</i>	46	24.7	4.5	0.23	1.8	A	S
<i>Megarhynchus pitangua</i>	71	24.0	3.9	0.31	1.7	A	S
<i>Myiozetetes granadensis</i>	29	22.1	3.6	0.20	1.8	A	S
<i>Elaenia flavogaster</i>	24	19.2	6.0	0.21	1.6	A	S
<i>E. frantzii</i>	20	22.6	5.5	0.18	1.8	A	S
<i>Tyranniscus vilissimus</i>	9	18.9	4.3	0.16	1.7	A	S
<i>Mionectes oleaginea</i>	11	24.5	4.2	0.17	1.5	A	S
<b>Mimidae</b>							
<i>Dumatella carolinensis</i>	39	14.0	8.4	0.25	1.7	P	S
<i>Mimus polyglottos</i>	51	16.0	9.7	0.24	1.7	P	S

TABLE 3  
CONTINUED

	Body weight (g)	Flight muscles (% body weight)	Leg muscles (% body weight)	Wing loading (g/cm <sup>2</sup> )	Aspect ratio (span/chord)	FCM <sup>3</sup>	FHM <sup>4</sup>
<b>Muscicapidae, Turdinae</b>							
<i>Turdus plebejus</i>	87	22.0	7.6	0.30	1.9	P	S
<i>Myadestes melanops</i>	32	18.7	4.8	0.24	1.7	P	S
<i>Catharus ustulatus</i>	33	19.6	5.6	0.24	1.9	A/P	S
<b>Bombycillidae</b>							
<i>Bombycilla cedrorum</i>	33	22.6	4.0	0.29	2.1	P	S
<b>Vireonidae</b>							
<i>Vireo olivaceus</i>	17	18.6	5.9	0.18	1.9	P	S
<b>Emberizidae, Parulinae</b>							
<i>Vermivora peregrina</i>	9	17.1	6.6	0.15	1.9	P	S
<i>Dendroica pennsylvanica</i>	10	15.2	7.0	0.14	1.9	P	S
<b>Icterinae</b>							
<i>Zarhynchus wagleri</i>	163	17.2	9.4	0.34	2.0	P	S
<i>Cacicus uropygialis</i>	59	15.6	9.9	0.26	1.7	P	S
<i>Icterus galbula</i>	34	18.0	8.1	0.24	1.8	P	S
<b>Thraupinae</b>							
<i>Chlorophanes spiza</i>	18	18.8	8.1	0.23	1.7	P	M
<i>Cyanerpes lucidus</i>	13	17.5	7.0	0.22	1.8	P	M
<i>Dacnis venusta</i>	16	22.1	6.3	0.21	1.8	P	M
<i>Chlorophonia callophrys</i>	25	18.3	7.2	0.30	1.8	P	M
<i>Euphonia luteicapilla</i>	12	18.2	5.2	0.25	1.8	P	M
<i>E. imitans</i>	13	17.6	6.1	0.20	1.7	P	M
<i>Tangara larvata</i>	19	21.5	6.1	0.21	1.7	P	M
<i>T. guttata</i>	20	17.8	9.3	0.26	1.7	P	M
<i>Thraupis episcopus</i>	32	20.9	6.9	0.25	1.8	P	M
<i>T. palmarum</i>	39	20.8	—	0.26	1.6	P	M
<i>Piranga rubra</i>	30	19.1	5.6	0.22	1.9	P	M
<i>P. olivacea</i>	31	20.1	5.7	0.19	2.0	P	M
<i>Tachyphonus luctuosus</i>	15	16.1	6.0	0.19	1.6	P	M
<i>T. rufus</i>	35	17.4	9.9	0.25	1.6	P	M
<i>Ramphocelus dimidiatus</i>	30	15.9	7.4	0.25	1.6	P	M
<i>R. passerinii</i>	32	18.3	8.4	0.30	1.6	P	M
<i>Habia rubica</i>	36	18.8	8.8	0.25	1.5	P	M
<i>H. fuscicauda</i>	39	16.4	8.7	0.22	1.6	P	M
<i>Chlorospingus ophthalmicus</i>	20	15.7	8.9	0.25	1.6	P	M
<b>Cardinalinae</b>							
<i>Saltator maximus</i>	48	18.4	8.2	0.26	1.5	P	M
<i>Passerina (Cyanocompsa) cyanoides</i>	32	19.0	6.8	0.31	1.5	P	M/Pr
<b>Emberizinae</b>							
<i>Arremonops conirostris</i>	40	14.5	13.0	0.34	1.5	P	M/Pr

<sup>1</sup> Data from Hartman 1961 except as noted. Values presented are averages for males and females where given separately by Hartman.

<sup>2</sup> Data for *Steatornis caripensis* from Snow 1961.

<sup>3</sup> FCM = fruit capture mode; A = in air; P = from perch.

<sup>4</sup> FHM = fruit handling mode; S = swallow whole; M = mash; Pr = seed predator.

groups of fruit-eating birds encourage the search for general functional relationships between wing morphology and feeding behavior.

If frugivores can be fit into a functional-morphological space (see James 1982), then we offer three examples from Costa Rica that represent three extremes of that space and that will serve to illustrate the morphological adaptations and behavioral consequences that characterize



FIG. 7. Wing outlines of (A) *Querula purpurata*, (B) *Trogon massena*, and (C) *Pteroglossus torquatus* drawn to approximately same scale from photographs of birds in flight.

frugivores within that space. The Collared Aracari, the Slaty-tailed Tropicbird, *Trogon massena*, and the Purple-throated Fruit-crow represent three divergent types of wing morphology and feeding behavior of frugivores (Fig. 7). Because of the marked aerodynamic constraints imposed by increasing size (Pennycuick 1969; Kokshaysky 1973; Greenewalt 1975; Norberg 1981), these relatively large birds (>100 g) may better illustrate the limiting cases, at least as far as the aerial feeders are concerned.

*Querula purpurata* obtains most of its fruits by swooping, although snatching and picking are used (Snow 1971b; pers. observ.; Fig. 4). *Trogon massena* takes its fruits by stalling (we have never seen it hover); and *Pteroglossus torquatus* obtains nearly all its food by picking and reaching (rarely using snatching) (Santana C., Moermond, and Denslow, unpubl. data; Fig. 4). The morphological differences in the species correspond to differences in feeding behavior. *Querula* has the lowest wing loading of any bird of its size for which data are available (Table 3; Snow 1982: fig. 1). While all three birds have relatively long wings, *Querula* has unusually wide wings mainly due to the broad, long secondaries and shows a relatively small degree of slotting at the wing tips (Fig. 7). This very broad wing allows these birds to make long, relatively slow, swooping flights to pluck fruits, one at a time. By comparison, *Trogon massena* has a narrower wing (higher aspect ratio) with very prominent, deep square slots. This slotting pattern allows the trogon to fly very slowly before stalling. Its flight pattern consists of a rise, followed by an abrupt slowing until it stalls and drops. Fruits are plucked singly at the top of the rise at the point of stalling. This type of flight is likely facilitated by extreme slotting of the primaries as well as by well-developed flight muscles and heart (Table 3; Hartman 1961; Moermond and Santana C., unpubl. data). The unusually large, broad tail of the trogon (see Hartman 1961) is spread during stalling and may aid in braking or in controlling the precise moment of the stall.

In contrast to these two aerial feeders, *Pteroglossus torquatus* appears to have difficulty flying slowly. Its wing loading is high, and it has poorly developed V-shaped slots that may

operate effectively only when the wing is under maximum stress, as in take-off (pers. observ.). These toucanets usually fly from tree to tree in a straight line with rapid wing beats and relatively high impact landings. In comparison to *Querula* or *Trogon*, the toucanet's velocity range is narrower and its horizontal cruising velocity faster, as expected for a bird with high wing loading (cf. Pennycuick 1969, 1975). Correlated with better reaching ability, leg musculature of *Pteroglossus* is considerably heavier than that of the trogon or fruit-crow (Table 3).

The morphological differences between the toucanet and the two aerial species are marked and correspond well with differences in fruit-taking behavior and fruit choice described in earlier sections; however, the strong morphological differences between the trogon and fruit-crow are more surprising given that both species take fruit primarily on the wing. Nonetheless, the differences in their feeding techniques likely have consequences for fruit selection. The trogon's flight style is characterized by expensive powered flapping; the fruit-crow's swooping glides may provide cheaper flight and lower costs of plucking its fruit. Trogons, however, appear better at negotiating small spaces in the understory and lower parts of tree crowns, while the fruit-crow forages more often (and presumably more efficiently) among the larger open spaces of the canopy and takes more fruits from the upper portions of trees.

Field observations of similar birds at Monte Verde, Costa Rica (Snow 1977; Wheelwright 1983; Santana C. and Milligan 1984) provide strong support for the patterns we observed in the lowland birds listed above. Observations of the Resplendent Quetzal (*Pharomachrus mocinno*), and the Three-wattled Bellbird (*Procnias tricarunculata*), a large, broad-winged cotinga, feeding in the same trees show that *Pharomachrus* take fruit primarily from the lower portions of the trees whereas the bellbirds take significantly more fruits from the upper portions of the trees (Santana C. and Milligan 1984). Compared to *Querula*, the bellbird does not appear to be as specialized for aerial flight, having a shorter wing, likely higher wing loading, and relatively longer (and stronger?) legs (Snow 1982). The bellbird often is able to pick and reach some fruit from a perch (Snow 1977; Santana C. and Milligan 1984) but frequently resorts to taking fruit on the wing if the fruits are not easily accessible or are difficult to remove (Snow 1977). The two toucans at Monte Verde, *Aulacorhynchus prasinus* and *Ramphastos sulfuratus*, pick or reach virtually all their food items. The *Ramphastos*, which are much heavier than the *Aulacorhynchus*, are "able to pluck every fruit they reach out for and grasp with their mandibles, so they hardly move at all while feeding" (Snow 1977:628).

The small wing area and deep slotting of both *Manacus* and *Phoenicircus* suggest wing movements and flight behavior similar to those described for *Trogon massena* above. The relatively longer wing of *Pipra mentalis* and other small manakins may improve their hovering abilities and lower other flight costs (cf. Norberg 1981). Other examples with relatively minor but, nevertheless, noticeable, differences in wing shape invite further analysis.

**Legs.**—Legs are the other major morphological feature influencing manner of capture and selection of fruits. Although muscle weights are seldom taken, Hartman's data (1961; Table 3) show considerable interspecific variation in the percent of body weight in leg muscles. The leg musculature of trogons accounts for only about 3 percent of their body weight (2.7–3.2 percent for 7 *Trogon* spp. and 3.4 percent for *Pharomachrus*), and their feet are so weak that the birds may be unable to turn around on a perch without using their wings (Santana C., Moermond, and Denslow, unpubl. data). Many other species, however, have two to four times as much of the body weight in leg muscles (e.g., Ramphastidae and tanagers, Table 3). In the absence of functional analyses, we assume that birds with a greater percentage of body weight in leg musculature have stronger legs.

Species with strong legs fall into two fairly distinct functional groups: ground feeding birds, such as most thrushes (e.g., *Catharus* spp. and *Turdus* spp.) and emberizines (e.g., *Arremon* and *Arremonops* spp.), and perching birds, such as many tanagers and honeycreepers, that reach food items from perches on narrow branches (see previous section).

Relative tarsal lengths differ in the two groups of strong-legged species. Those birds that often perch or feed on the ground have longer tarsi than similar species that feed primarily above the ground; this pattern has been observed within diverse groups of birds (Dilger 1956; Newton 1967; Fretwell 1969; Partridge 1976; Fitzpatrick 1978). The tarsi of birds that perch primarily on branches vary in length and diameter depending on their feeding behavior. Among tyrannid flycatchers, aerial feeders using perches for resting have short tarsi, while those that feed by gleaning from perches have long, narrow tarsi (Fitzpatrick 1978). The long legs of perch-gleaners are presumed to increase the visible scanning area and to facilitate clinging to angled perches (Fitzpatrick 1978). Few tyrannids, however, reach below their perch level.

Species that reach down from perches tend to have shorter and thicker tarsi (Grant 1965, 1966; Sturman 1968; Moermond, Howe, Bruskewitz, and Rusterholz, unpubl. data; see Partridge 1976 and references therein).

Among frugivores, species with the "ground" type legs are able to reach out or down from perches only with difficulty. Our aviary experiments with two such species (*Catharus minimus* and *Arremon aurantiirostris*) have shown that these birds would rather jump up to hanging fruits that reach down when fruits are further than a few centimeters below a perch (Denslow and Moermond, in press, unpubl. data). Species with strong legs of the "perching" type are usually agile on small diameter perches and able to reach below their perch to pluck fruits. Many of the smaller tanagers and honeycreepers appear able to reach well below a perch. As in hovering ability, small absolute size facilitates such behavior (Newton 1967). Nevertheless, not all small birds reach equally well. *Thraupis palmarum*, for example, can reach its full body length below a perch, while the somewhat smaller *Ramphocelus passerini* cannot do so without apparent difficulty (Denslow and Moermond, in press, unpubl. data). The *Thraupis*, a heavier bird, has a distinctly shorter but thicker tarsus than the *Ramphocelus*.

Additional morphological features may enhance the reaching abilities of "perchers" (Osterhaus 1962; Leisler and Thaler 1982). Snow and Snow (1971) noted aspects of the foot, such as grip strength and claw shape, that may enhance the reaching ability of *Thraupis palmarum*. They also noted that *T. palmarum* and *Tangara guttata*, which frequently foraged by clinging head-down, had longer tails than their sympatric congeners. We have also noted in our aviary experiments that the long tail of *Saltator maximus* appears to aid in balance, allowing this species to forage in hanging positions on thin stems or leaves.

Reaching ability may be constrained by perch diameter. We have observed that a small bird such as *Euphonia gouldi* will reach readily from a 3 mm diameter perch but reluctantly from a 12 mm diameter perch (Moermond and Denslow 1983). A study of the ability of two paruline warbler species to reach from a series of perches demonstrated a considerable difference in distance reached over a relatively small range of perch diameters (3 mm–24 mm) (Moermond, Howe, Bruskewitz, and Rusterholz, unpubl. data). Similar detailed studies of closely related species have shown that minor differences in leg dimensions are correlated with distinct differences in activity patterns and microhabitat (Dilger 1956 with thrushes; Pearson 1977 with antwrens; Leisler and Thaler 1982 with Kinglets). These studies suggest that the variations in tarsal length and leg muscle mass described for fruit-eating birds are associated with differences in ability to negotiate different substrates and to pluck fruits presented on infructescences of different structure.

Among medium to large tanagers (Table 3), species that forage in the canopy or outer edges of vegetation (*Piranga rubra*, *P. olivacea*, *Thraupis episcopus*, *T. palmarum*, *Tachyphonus luctuosus*) have lower wing loading, higher aspect ratios, a higher percent of body weight in flight muscles, and a lower percent of body weight in their legs muscles than most species that frequently forage on or near the ground and in low vegetation (*Tachyphonus rufus*, *Ramphocelus passerini*, *R. icteronotus*, *Habia rubica*, *H. fuscicauda*). Among the canopy tanagers, the ones with the best reaching ability (*Thraupis* spp.) have the highest percent of body weight in their lower extremities, although the percentage is still below that shown by the "low vegetation and ground" species.

The suite of morphological features of a particular bird are expected to determine the relative accessibility of and the costs of taking available fruits and, thus, to influence strongly the bird's diet. While this is most clearly seen in such divergent birds as trogons and toucans, we believe it also contributes importantly to fruit choice among all fruit-eaters. Although species of diverse morphology often feed at the same fruiting tree (Eisenmann 1961; Land 1963; Willis 1966; Olson and Blum 1968; Leck 1969; Howe 1977; McDiarmid et al. 1977; Fig. 4), a discriminant function analysis of data from four of these studies was partially successful in separating groups of species on the basis of body, wing, and leg characteristics, although not of bill dimensions (Ricklefs 1977). Similarly, a multivariate analysis (Denslow and Moermond, in press) of 15 species of tanagers and honeycreepers studied by Snow and Snow (1971) demonstrated that these species could be separated by the species of fruits in their diets and that the differences among the bird groups appeared correlated with aspects of their morphology (bill size, percent body weight in leg muscles, wing loading). Likewise our aviary choice tests with 20 species of tanagers, manakins, thrushes, finches, and tyrannids have shown that all those tested exhibit clear, well-defined preferences for more accessible fruits with the differences in preferences

associated with differences in morphology (Moermond and Denslow 1983; Denslow and Moermond, in press, unpubl. data; Levey, unpubl. data).

A phylogenetic survey of frugivores shows, not surprisingly, that the members of each family are usually similar in morphology and similar in the techniques they use to take fruits (Table 3). Where important variation in locomotory morphology exists in these families, it is often associated with different techniques of fruit capture. The adaptive values of these patterns are apparent if one assumes that fruits presented in different ways actually constitute different resources. If certain morphological characteristics allow a bird to take some of these fruits more cheaply than others, then selection on such morphological adaptations may be enhanced. The presence of frugivorous species in so many families is not evidence for lack of requirements for eating fruits but rather represents adaptive "specialization" to exploit fruits displayed in different ways.

#### SPECIALISTS, GENERALISTS, AND SEED DISPERSAL

Snow (1980) designated as fruit specialists those species that can survive entirely on fruit and rear their young mainly on fruit. Such species (Oilbirds, a few cotingids) represent a small subset of the total range of fruit-eating birds that still may be classed as "legitimate" frugivores, i.e., species that digest the fruit pulp or juices but not the seed (Snow 1980). A further division of this large group of "legitimate" frugivores into specialist and generalists would be difficult and beset with contradictions and inconsistencies. For example, although large, lipid-rich fruits are taken primarily by large frugivores, these same birds generally take many species of small fruits also. By virtue of their sizes, the large frugivores (including those usually considered specialists) are certainly capable of taking the largest size range of fruits and, therefore, the largest number of fruit species (Wheelwright in press; Table 2, Fig. 1). In addition, morphological specializations for fruit-eating have been noted for only a few species, but include both large and small birds (e.g., Oilbirds and euphonias). Specializations in bill, wing, and leg morphology that affect methods of removal of fruits can be identified in several species among both traditional specialists and generalists. Finally, the "high quality" seed dispersal said to be associated with specialists is not necessarily characteristic of all birds traditionally called specialists (Oilbirds leave many seeds on the floor of their roosting caves), and, in addition, many traditional generalists appear to be good seed dispersers (e.g., Leck 1972a; Howe and DeSteven 1979; Greenberg 1981). With the exception of a few species that appear to be total frugivores, there does not seem to be sufficient basis in behavior, morphology, or function on which to recognize generalists and specialists among frugivorous birds.

As Wheelwright and Orians (1982) pointed out, the quality of seed dispersal for a given plant is likely to depend on a variety of factors and is not easily predicted just from the species of birds feeding on the plant's fruits. Safe sites for seed germination are not likely recognizable by the birds and in any case a "disperser" (in contrast to a pollinator) is "rewarded" for taking the seed but not for delivering it. Adaptive strategies for seed dispersal are more likely to involve simply moving as many seeds as possible from the immediate vicinity of the parent tree (Denslow 1980). Co-evolution among fruiting plants and their dispersers has very obviously occurred as evidenced in the characteristics of fruit displays (Van der Pijl 1969), but a better understanding of the interaction at the species level must take into account the factors influencing fruit selection by the dispersers.

The birds' choice of fruits is neither confined to specific fruits nor is it dictated only by chance of encounter. Experiments with a number of species of small and two species of large frugivores have shown that the birds make systematic decisions and that their choices depend on such factors as fruit size, pulp-to-seed ratio, ripeness, color, taste, and importantly, accessibility of the fruits from a perch and the distance between fruit clusters (Best 1981; Herrera 1981; Sorensen 1981; Moermond and Denslow 1983; Denslow and Moermond, in press; Levey et al. 1984; Santana C., Moermond, Denslow, unpubl. data).

Of most interest among the aviary experiments are choices in which a bird is induced to change an initial fruit preference by a change in one of the conditions under which the preferred fruit is offered (for example, a decrease in the accessibility of the preferred fruit or an increase in the flight distance to the preferred fruit). Such changes in preference have been observed in each of the frugivores we have studied so far, leading us to believe that fruit choice in the field is a dynamic process, i.e., the species and quantities of fruits taken are contingent upon the context within which each fruit is found (e.g., Best 1981; Levey et al. 1984).

Differences in fruits taken by different frugivores living in the same habitat may be attributed to differences in the birds' morphological abilities and physiological requirements that translate into differences in the benefit : cost balance associated with a given choice. The morphological and behavioral differences among frugivores are assumed to influence not only number and species of fruits eaten but also to influence the quality of dispersal of seeds. For example, very small seeds, such as those of Melastomataceae or *Ficus*, are easily passed through the digestive tract of large and small frugivores. Dispersal of larger seeds, however, is increasingly limited by their size. Not only may they be swallowed only by birds with sufficiently large gapes, but small and medium-sized birds (tanagers and finches) mash the fruits before swallowing them, often dropping the seeds at or near the parent plant. Thus, it may be advantageous for a tree producing medium to large seeds to display fruits in such a way as to lower the probability of removal by birds in this group. Because these birds are perching birds, display of fruits at the ends of long peduncles or at the tips of narrow flexible twigs, in effect, lowers their accessibility (Snow 1977; Denslow and Moermond, in press). Such fruit displays may also even enhance their probability of removal by aerial-feeding, fruit-swallowing birds (Denslow and Moermond 1982, in press; Santana C., Moermond, and Denslow, unpubl. data).

We suggest that the key to understanding such differences among fruit-eating birds lies in the constraints of morphology on behavior. Differences in digestive systems, bill strength and shape, wing and leg morphology, and body weight differentially affect the accessibility of fruits, the ease with which they are handled, the rates at which they are eaten, and the efficiency with which they are digested. Such constraints are expected to influence the birds' choices of fruits, the benefits and costs of taking those fruits, and ultimately, the fruiting patterns and display structures of plants competing for birds as dispersers.

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