# Tropical Fruit-eating Birds and their Food Plants: A Survey of a Costa Rican Lower Montane Forest[1]

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## ABSTRACT

In the lower montane forests of Monteverde, Costa Rica, at least 70 bird species rely on fruits to different degrees. We present over 700 records of birds feeding on the fruits of 171 plant species in a survey of a single site intended to complement Snow's (1981) world survey of fruit-eating by birds. The frequency with which birds visited plants and the characteristics of the fruits (dimensions, color patterns, nutritional traits) are also described. The number of bird species recorded feeding on the fruits of a particular plant species was positively correlated with the size of the plant and with its commonness. Because biases may also be introduced by observing plant species for different amounts of time, we distinguish those plant species that were thoroughly studied from others studied only casually. Plants in five genera (*Acnistus, Citharexylum, Ficus, Hampea,* and *Sapium*) attract more than 20 bird species; at about half of all plant species, we observed fewer than three bird species. These results should lead to a better understanding of the characteristics of neotropical fruits and the diets of fruit-eating birds.

## RESUMEN

En los bosques montano-bajos de Monteverde, Costa Rica, 70 especies de aves, por lo menos, dependen de frutos, en diferentes grados. Presentamos más de 700 observaciones de aves alimentándose de los frutos de 171 especies de plantas en un estudio efectuado en un solo lugar con la intención de complementar el estudio de Snow (1981) a nivel mudial sobre frugivoriá en aves. Se describen también la frecuencia con que las aves visitaban las plantas y las características de los frutos (dimensiones, patrones de color, composición nutritional). El número de especies de aves que notamos comiendo frutos de una especie en particular resultó positivamente relacionado con el tamaño de la planta y con su abundancia. Como esta correlación también dependía de la durción de la observación de cada especie de planta, distinguimos entre las especies que estudiamos cuidadosamente o solamente casualmente. Las plantas de cinco géneros (*Acnistus, Citharexylum, Ficus, Hampea,* y *Sapium*) atrayeron más de 20 especies de aves; en aproximadamente la mitad de todas las especies de plantas observamos menos de tres especies de aves. Estos resultados permiten un mejor entendimiento de las características de los frutos neotropicales y de las dietas de las aves frugívoras.

AFTER SUBSTANTIAL FIELD RESEARCH stimulated by the theoretical papers of Snow (1971) and McKey (1975), most studies on fruit-eating birds have arrived at a similar conclusion: the factors governing diet choice and seed dispersal by birds are more complicated and elusive than originally believed (cf. Sorenson 1981, Howe and Vande Kerckhove 1979). In response to the complexity of the problem, researchers have taken distinct approaches. Studies differ in taxonomic focus (plants or birds), hierarchical focus (individuals, species, guilds, or communities), and method (comparative, experimental or theoretical). Each has made significant contributions (for a review see Howe and Smallwood 1982).

There are clear tradeoffs between breadth of focus and depth of results. Most researchers have favored more detailed studies by concentrating on individual plant or bird populations (Howe 1977, Howe 1981, Herrera 1981, Wheelwright 1983), although others have examined groups of interacting or ecologically similar species (Wheelwright 1984, Jenkins 1969) or simple communities (Sorensen 1981, Baird 1980). As a result, however, literature syntheses have had to rely on information as-

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TABLE 1. *Fruit-eating birds of Monteverde, Costa Rica.*

| Family | Code | Common name | Scientific name | Gape width (mm) |
|---|---|---|---|---|
| Cracidae | BG[b] | Black Guan | *Chamaepetes unicolor* | 31.0 |
| Columbidae | BP[b] | Band-tailed Pigeon | *Columba fasciata* | 10.0 |
| | RP | Red-billed Pigeon | *C. flavirostris* | 10.0 |
| | DP | Ruddy Pigeon | *C. subvinacea* | 10.0 |
| | SP | Short-billed Pigeon | *C. nigrirostris* | 9.5 |
| | WD | White-tipped Dove | *Leptotila verreauxi* | 9.5 |
| Cuculidae | GA | Groove-billed Ani | *Crotophaga sulcirostris* | 13.5 |
| | SC | Squirrel Cuckoo | *Piaya cayana* | — |
| Trogonidae | RQ[a] | Resplendent Quetzal | *Pharomachrus mocinno* | 21.0 |
| | OT[b] | Orange-bellied Trogon | *Trogon aurantiiventris* | 17.0 |
| Momotidae | BM | Blue-crowned Motmot | *Momotus momota* | 19.0 |
| Capitonidae | RB | Red-headed Barbet | *Eubucco bourcierii* | — |
| | PB[b] | Prong-billed Barbet | *Semnornis frantzii* | 17.0 |
| Ramphastidae | ET[a] | Emerald Toucanet | *Aulacorhynchus prasinus* | 26.0 |
| | KT[b] | Keel-billed Toucan | *Ramphastos sulfuratus* | 31.0 |
| Picidae | GW | Golden-olive Woodpecker | *Piculus rubiginosus* | 11.5 |
| | FW[b] | Golden-fronted Woodpecker | *Melanerpes aurifrons* | 15.0 |
| | SW | Smoky-brown Woodpecker | *Veniliornis fumigatus* | — |
| Pipridae | LM[a] | Long-tailed Manakin | *Chiroxiphia linearis* | 8.5 |
| Cotingidae | FP | Rufous Piha | *Lipaugus unirufus* | — |
| | MT[b] | Masked Tityra | *Tityra semifasciata* | 18.0 |
| | TB[a] | Three-wattled Bellbird | *Procnias tricarunculata* | 25.0 |
| | CD | Cinnamon Becard | *Pachyramphus rufus* | — |
| Tyrannidae | TK[b] | Tropical Kingbird | *Tyrannus melancholicus* | 16.0 |
| | SF | Sulfur-bellied Flycatcher | *Myiodynastes luteiventris* | 17.0 |
| | GF | Golden-bellied Flycatcher | *M. hemichrysus* | 15.5 |
| | BF | Boat-billed Flycatcher | *Megarhynchus pitangua* | 16.5 |
| | CF | Social Flycatcher | *Myiozetetes similis* | 13.0 |
| | DF | Dusky-capped Flycatcher | *Myiarchus tuberculifer* | 12.0 |
| | YE | Yellow-bellied Elaenia | *Elaenia flavogaster* | 10.0 |
| | ME[b] | Mountain Elaenia | *E. frantzii* | 8.5 |
| | OF[b] | Olive-striped Flycatcher | *Mionectes olivaceus* | 8.5 |
| | YC[b] | Yellowish Flycatcher | *Empidonax flavescens* | 9.0 |
| Corvidae | BJ[b] | Brown Jay | *Psilhorinus morio* | 21.0 |
| Muscicapidae | BS[a] | Black-faced Solitaire | *Myadestes melanops* | 11.0 |
| | WR[b] | White-throated Robin | *Turdus assimilis* | 10.0 |
| | CR[b] | Clay-colored Robin | *T. grayi* | 14.0 |
| | MR[a] | Mountain Robin | *T. plebejus* | 12.0 |
| | ST[a] | Swainson's Thrush | *Catharus ustulatus* | 10.5 |
| | RN | Ruddy-capped Nightingale-Thrush | *C. frantzii* | — |
| | BN | Black-headed Nightingale-Thrush | *C. mexicanus* | 10.5 |
| | ON | Orange-billed Nightingale-Thrush | *C. aurantiirostris* | 9.5 |
| Ptilogonatidae | BY[a] | Black-and-yellow Phainoptila | *Phainoptila melanoxantha* | 11.5 |
| Vireonidae | SV | Solitary Vireo | *Vireo solitarius* | 8.5 |
| | YV | Yellow-green Vireo | *V. flavoviridis* | 8.0 |
| | BV | Brown-capped Vireo | *V. leucophrys* | — |
| Emberizidae | CO | Chestnut-headed Oropendola | *Zarhynchus wagleri* | 18.0 |
| | BC | Bronzed Cowbird | *Molothrus aeneus* | 11.5 |
| | NO | Northern Oriole | *Icterus galbula* | 10.0 |
| | RH | Red-legged Honeycreeper | *Cyanerpes cyaneus* | 7.0 |
| | SD | Scarlet-thighed Dacnis | *Dacnis venusta* | 8.0 |
| | GC[b] | Golden-browed Chlorophonia | *Chlorophonia callophrys* | 6.5 |
| | YT | Yellow-throated Euphonia | *Euphonia hirundinacea* | 7.0 |
| | TT | Silver-throated Tanager | *Tangara icterocephala* | 9.0 |
| | CT | Spangle-cheeked Tanager | *T. dowii* | 9.0 |
| | GT[b] | Blue-gray Tanager | *Thraupis episcopus* | 10.0 |
| | PT | Palm Tanager | *T. palmarum* | 10.5 |
| | HT | Hepatic Tanager | *Piranga flava* | 12.5 |
| | UT | Summer Tanager | *P. rubra* | 11.0 |
| | CB[a] | Common Bush-Tanager | *Chlorospingus ophthalmicus* | 10.0 |
| | SB | Sooty-capped Bush-Tanager | *C. pileatus* | 9.5 |

TABLE 1. *(Continued).*

| Family | Code | Common name | Scientific name | Gape width (mm) |
|---|---|---|---|---|
| | TS | Buff-throated Saltator | *Saltator maximus* | 18.5 |
| | GS | Grayish Saltator | *S. coerulescens* | 14.5 |
| | RG | Rose-breasted Grosbeak | *Pheucticus ludovicianus* | — |
| | YG | Yellow-faced Grassquit | *Tiaris olivacea* | 6.5 |
| | WS | White-eared Ground-Sparrow | *Melozone leucotis* | 12.5 |
| | YF | Yellow-throated Brush-Finch | *Atlapetes gutturalis* | 10.5 |
| | CC | Chestnut-capped Brush-Finch | *A. brunneinucha* | — |
| | RS[b] | Rufous-naped Sparrow | *Zonotrichia capensis* | 8.0 |
| | YH | Yellow-thighed Finch | *Pselliophorus tibialis* | — |

[a] Species studied in detail; fruit diet at Monteverde believed to be well represented in Table 2.
[b] Species studied less systematically; fruit diet at Monteverde moderately well known. Other species not studied systematically; feeding records represent miscellaneous observations.

sembled from disparate studies in different habitats in their attempts to derive general principles (Ricklefs 1977, Stiles 1980, Herrera 1981, Thompson 1982). How well does the sampling of a diverse literature reflect actual patterns of frugivory in communities? As a follow-up to Snow's (1981) world survey of fruit-eating by birds, we present observations from a single site to allow an evaluation of the generality of such surveys. Over 700 feeding records gathered over a five-year period involve 70 bird species and 171 plant species from a lower montane wet/rain forest in Costa Rica. Descriptions (color, dimensions, nutrients) of the fruits eaten by birds accompany feeding records.

## STUDY SITE AND METHODS

Our study area, Monteverde, Costa Rica (10°18′N, 84°48′W), lies on a relatively flat plateau at an elevation of 1350–1550 m. Its western border falls steeply to the Pacific lowlands; to the east it is bounded by the continental divide and the Atlantic slope. Rainfall, which occurs mainly between May and December, exceeds 2400 mm in most years ($\bar{x}$ = 2485 mm). Because of the sharp moisture gradient caused by the prevailing NE trade winds passing over the divide, forest structure and species composition change markedly along the plateau within a 4 km distance from the "elfin" cloud forest on the divide to the taller, moist forest on the western edge of the plateau (see Lawton and Dryer 1980, for a more complete description of the site). Our observations were restricted to the 2700 ha Monteverde Cloud Forest Reserve, the surrounding forests, and the woodlots and pastures of the community itself (total area ca. 15 km$^2$).

WAH and CG initiated the study in late 1978 by noting feeding records during their forest phenology study. In 20 months of field work from 6/79 until 8/83, NTW collected records using various techniques: seed-trapping beneath the display or nest perches of certain species (Wheelwright 1983; cf. Snow 1970); observing and conducting censuses at fruiting trees (cf. Howe 1977), especially 15 species in the Lauraceae; following foraging flocks and monitoring food deliveries to nestlings; and recording miscellaneous observations. From 6/81 to 7/83 KGM tracked radio-collared birds to fruiting plants, collected fecal samples from mist-netted birds, and noted miscellaneous feeding records, particularly in the lower montane rain forest. Additional observations were shared by other biologists working at Monteverde (R. and M. Laval, W. Busby, P. Feinsinger, K. Winnett-Murray, pers. comm.). With taxonomic help from the Chicago Field Museum and the Missouri Botanical Garden, WAH identified most of the plant species.

Gape widths of birds, measured at the commissural points on museum specimens from the Harvard Museum of Comparative Zoology and the Yale Peabody Museum of Natural History, are expressed as means of the samples, which included at least one male and one female/species ($N$ = 2–9 individuals/species). Fruit characteristics were determined on a sample of representative fruits from 1–20 individual plants. We used calipers to measure fresh fruit length and diameter, and a spring balance to determine fresh mass. Nutritional analyses were performed by the Palmar Plant and Soils Laboratory at the University of Alaska. Sugar concentration was estimated from crushed fruit pulp spread on a Bausch and Lomb pocket refractometer. Sample sizes vary in different analyses because we were unable to record complete information for all plant species.

## SAMPLING BIASES

Before presenting results, we should discuss the potential biases of using various methods in this and other studies. Because of different research emphases and techniques, the feeding records presented below underrepresent certain groups of birds and plants and overrepresent others.

TABLE 2. *Fruit species eaten by birds of Monteverde, Costa Rica.*

| Plant species | Bird species[a] | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BG | BP | RP | RQ | OT | BM | PB | ET | KT | GW | FW | LM | MT | TB | SF | BF | CF |
| Subclass Magnoliidae | | | | | | | | | | | | | | | | | |
| ANNONACEAE | | | | | | | | | | | | | | | | | |
| [c] *Guatteria consanguinea* | o | | | c | | | | c | | | | | | | | | |
| MONIMIACEAE | | | | | | | | | | | | | | | | | |
| *Siparuna* sp. A | | | | | | | | | | | | | | | | | |
| LAURACEAE | | | | | | | | | | | | | | | | | |
| [c] *Beilschmiedia costaricensis* | u | | | c | | | | c | o | | | | | c | | | |
| *B.* sp. BL | | | | | | | | o | | | | | | | | | |
| [c] *B.* sp. BC | c | | | c | | | | c | | | | | | c | | | |
| [c] *Nectandra davidsoniana* | o | | | c | | | | c | o | | | | o | c | | | |
| [c] *N. gentlei* | u | | | u | | | | c | | | | | | u | c | o | |
| [c] *N. hypoglauca* | u | | | c | | | | c | c | | | | | c | | | |
| [c] *N. salicina* | u | | | c | | | | c | c | | | | | c | | | |
| *N.* sp. NC | | | | o | | | | | | | | | | c | | | |
| *N.* sp. NG | | | | | | | | o | u | | | | | | | | |
| [c] *Ocotea austinii* | | | | c | | | c | c | | | | | | c | | | |
| [c] *O. bernouliana* | | | | o | | | | c | u | | | | | o | | | |
| [c] *O. klotzschiana* | | | | u | | | | c | | | | | | | | | |
| [c] *O. tonduzii* | c | | | c | u | | c | c | c | | | u | c | c | c | c | |
| [c] *O. wachenheimii* | c | | | c | | | | c | c | | | | | c | | | |
| [c] *O.* sp. FL | c | | | c | | | | c | | | | | | c | | | |
| [c] *O.* sp. K2 | u | | | c | | | | c | | | | | | c | | | |
| [d] *O.* sp. RP | u | | | c | | | | c | | | | | | c | | | |
| [d] *Persea veraguensis* | | | | | | | | o | | | | | | | | | |
| *P.* FL | | | | | | | ? | | | | | | | | | | |
| *P.* RS | | | | ? | | | | | | | | | | | | | |
| [c] *Phoebe mexicana* | | | | c | | | | c | c | | | | c | c | | | |
| [c] *P. neurophylla* | | | | c | u | | | c | o | | | | c | c | | | |
| PIPERACEAE | | | | | | | | | | | | | | | | | |
| [d] *Piper auritum* | | | | | | | | u | | | | | | | | | |
| *Piper* sp. A | | | | | | | | | | | | o | | | | | |
| SABIACEAE | | | | | | | | | | | | | | | | | |
| *Meliosma idiopoda* | u | | | | | | | o | | | | | | | | | ? |
| PAPAVERACEAE | | | | | | | | | | | | | | | | | |
| [d] *Bocconia frutescens* | | | | | | | | | | | | o | | | | | |
| Subclass Hamamelidae | | | | | | | | | | | | | | | | | |
| ULMACEAE | | | | | | | | | | | | | | | | | |
| [c] *Trema micrantha* | | c | | | o | | | c | | | | | | o | | c | c |
| MORACEAE | | | | | | | | | | | | | | | | | |
| [c] *Ficus pertusa* | | | | c | | c | | c | | | | c | | c | | | |
| [c] *F. tuerckheimii* | o | o | | c | o | c | o | c | c | o | | c | c | c | | | |
| *Trophis mexicana* | | | | | | | | | | | | u | | | | | |
| CECROPIACEAE (MORACEAE) | | | | | | | | | | | | | | | | | |
| [d] *Cecropia obtusifolia* | | | | | | | o | c | | | | c | | | | | |
| URTICACEAE | | | | | | | | | | | | | | | | | |
| [d] *Urera elata* | c | | | | | | | c | c | | | | | | | | |
| Subclass Caryophyllidae | | | | | | | | | | | | | | | | | |
| PHYTOLACCACEAE | | | | | | | | | | | | | | | | | |
| *Phytolacca rivinoides* | | | | | | | o | | | | | | | | | | |
| *P.* sp. A | | | | | | | | | | | | c | | | | | |

TABLE 2. *(Extended)*.

| Bird species[a] | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DF | YE | ME | OF | BJ | BS | WR | CR | MR | ST | BY | SD | NO | GC | YT | TT | CT | GT | UT | CB | RG | WS | YF | Total[b] |
| | | | | | | | | u | | | | | | | | | | | | | | | 4 |
| | | | c | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 5 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 4 |
| | | | | | | | | c | | | | | | | | | | | | | | | 7 |
| | | | | | o | | | c | | | | | | | | | | | | | | | 8 |
| | | | | | | | | | | | | | | | | | | | | | | | 5 |
| | | | | | | | | | | | | | | | | | | | | | | | 5 |
| | | | | | | | | | | | | | | | | | | | | | | | 2 |
| | | | | | | | | | | | | | | | | | | | | | | | 2 |
| | | | | | | | | c | | | | | | | | | | | | | | | 5 |
| | | | | | | | | | | | | | | | | | | | | | | | 4 |
| | | | | | | | | o | | | | | | | | | | | | | | | 3 |
| | | | | | o | c | u | c | c | | | | | | | | | | | | | | 18 |
| | | | | | | | | | | | | | | | | | | | | | | | 5 |
| | | | | | | | | | | | | | | | | | | | | | | | 4 |
| | | | | | | | | | | | | | | | | | | | | | | | 4 |
| | | | | | | | | c | | | | | | | | | | | | | | | 5 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | — |
| | | | | | | | | c | | | | | | | | | | | | | | | 1 |
| | | | | | o | c | | c | c | | | | | | | | | | | | | | 9 |
| | | | | | | c | | c | | | | | | | | | | | | | | | 8 |
| | | | | | | | | | | | | | | | | | u | | | | | | 2 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | c | | | | | | | | | | | | | | | 3 |
| | | o | c | | | | | | | | | | | | | | | | | | | | 4 |
| o | | c | | | | | | c | c | | | u | | c | | | | | | o | c | o | 16 |
| | | | | o | | | | | | | | | c | | | | | | o | | | | 8 |
| | | | | c | o | o | | c | | | | o | c | o | | | | | o | | o | | 21 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | o | | | | | o | | | | o | | o | c | | o | | | | 10 |
| | | c | | | c | | o | u | | | | | c | | | c | | | c | | o | o | 13 |
| | | u | | | c | | | | | c | | | | | | | | | o | | | | 5 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |

TABLE 2. *(Continued).*

| Plant species | BG | BP | RP | RQ | OT | BM | PB | ET | KT | GW | FW | LM | MT | TB | SF | BF | CF |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bird species[a] | | | | | | | | | | | | | | | | |
| NYCTAGINACEAE | | | | | | | | | | | | | | | | | |
| *Neea amplifolia* | | | | | | | | ? | | | | ? | | | | | |
| *Torrubia costaricana* | | | | | | | | o | | | | | | | | | |
| Subclass Dilleniidae | | | | | | | | | | | | | | | | | |
| THEACEAE | | | | | | | | | | | | | | | | | |
| [c] *Symplocarpon brenesii* | | | | c | | | c | c | | | | | | c | | | |
| MARCGRAVIACEAE | | | | | | | | | | | | | | | | | |
| *Marcgravia brownei* | | | | | | | | c | | | | | | | | | |
| CLUSIACEAE (GUTTIFERAE) | | | | | | | | | | | | | | | | | |
| *Clusia alata* | | | | | | | c | c | | | | | | | | | |
| MALVACEAE | | | | | | | | | | | | | | | | | |
| [c] *Hampea appendiculata* | u | | | | | u | | c | | | o | c | c | o | | | |
| [d] *Malvaviscus arboreus* | | | | | | | c | c | | | | u | | | | | |
| FLACOURTIACEAE | | | | | | | | | | | | | | | | | |
| *Casearia sylvestris* | | | | | | | | | | | | | | o | | | |
| [c] *Hasseltia floribunda* | o | c | | c | c | | o | c | | | | c | o | c | | | |
| [a] *Xylosma chloranthum* | | | | | | | | c | | | o | | | | o | c | |
| *X. flexuosa* | u | | | | | | | o | | | | | | | | | |
| *X. intermedium* | | | | | | | | | | | | | | o | | | |
| CUCURBITACEAE | | | | | | | | | | | | | | | | | |
| sp. A | | | | | | | | o | | | | | | | | | |
| ERICACEAE | | | | | | | | | | | | | | | | | |
| *Cavendishia complectans* | | | | | u | | | | | | | | | | | | |
| *C. melastomoides* | | | | | | | | | | | | | | | | | |
| *C. capitulata* | | | | | | | | | | | | | | | | | |
| *C.* sp. A | | | | | | | | | | | | c | | o | | | |
| *Satyria* sp. A | | | | | | | | | | | | | | | | | |
| SAPOTACEAE | | | | | | | | | | | | | | | | | |
| *Dipholis parvifolia* | | | | ? | | | | | | | | | | ? | | | |
| SYMPLOCACEAE | | | | | | | | | | | | | | | | | |
| [c] *Symplocos limoncillo* | o | | | o | u | | | c | o | | | | | | | | |
| *S.* sp. A | | | | | | | u | | | | | | | | | | |
| *S.* sp. B | | | | o | | | | | | | | | | | | | |
| MYRSINACEAE | | | | | | | | | | | | | | | | | |
| *Ardisia compressa* | | | | | | | | c | | | | c | | | | | |
| [c] *A. palmana* | c | | | c | | | | c | | | | | | c | | | |
| [c] *Rapanea myricoides* | | | | | | | | c | u | o | c | | u | | | | c |
| Subclass Rosidae | | | | | | | | | | | | | | | | | |
| ROSACEAE | | | | | | | | | | | | | | | | | |
| [c] *Prunus anularis* | | | | | | | | c | c | | | | | | | | |
| *P.* sp. A | | | | | | | | c | | | | | | o | | | |
| *P. cornifolia* | | | | | | | | | | | | | | | | o | |
| [c] *Rubus rosaefolia* | | | | c | | o | c | o | | | | | | | | | |
| THYMELAEACEAE | | | | | | | | | | | | | | | | | |
| *Daphnopsis americana* | | c | c | | | | | o | | | | | | | | | |
| MYRTACEAE | | | | | | | | | | | | | | | | | |
| *Eugenia* sp. A | | | | | | | | o | | | | | | | | | |
| [c] *Eugenia* sp. B | | | | o | | | | | | | | | | | | | |
| sp. SC | | | | | | | u | | | | | | | | | | |

TABLE 2. *(Extended).*

| Bird species[a] | | | | | | | | | | | | | | | | | | | | | | | |
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| DF | YE | ME | OF | BJ | BS | WR | CR | MR | ST | BY | SD | NO | GC | YT | TT | CT | GT | UT | CB | RG | WS | YF | Total[b] |
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TABLE 2. *(Continued).*

| Plant species | Bird species[a] | | | | | | | | | | | | | | | | |
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| | BG | BP | RP | RQ | OT | BM | PB | ET | KT | GW | FW | LM | MT | TB | SF | BF | CF |
| MELASTOMATACEAE | | | | | | | | | | | | | | | | | |
| *Blakea grasilis* | | | | | | | | | | | | c | | | | | |
| [c] *Concostegia bernouliana* | | c | | o | o | | | o | | | | c | | o | o | | |
| *C. puberula* | | | | | | | | o | | | | | | | | | |
| *C. speciosa* | | | | | | | | | | | | | | | | | |
| *C. xalapensis* | | | | | | | | | | | | c | | | | | |
| *Miconia* sp. A | | | | | | | c | | | | | | | | | | |
| *Ossaea micrantha* | | | | | | | o | | | | | | | | | | |
| *O.* sp. A | | | | | | | o | | | | | | | | | | |
| sp. CT | | | | | | | | | | | | | | | | | |
| sp. NC | u | | | | | | | | | | | | | | | | |
| OLACACEAE | | | | | | | | | | | | | | | | | |
| *Linociera dominguensis* | | o | | | | | | o | | | | | | | | | |
| LORANTHACEAE | | | | | | | | | | | | | | | | | |
| *Gaiadendron punctatum* | | | | | | | | | | | | | | | | | |
| [d] sp. A | | | | | | | | | | | | | | | | | |
| sp. B | | | | | | | | | | | | | | | | | |
| CELASTRACEAE | | | | | | | | | | | | | | | | | |
| [d] sp. A | | | | | | o | | o | | | | | | | | | |
| [c] *Perrotettia longistylis* | | | | | | | | | | | | | | | | | |
| *Maytenus* sp. A | | | | | | | | | | | | | | | | | |
| AQUIFOLIACEAE | | | | | | | | | | | | | | | | | |
| [c] *Ilex lamprophylla* | c | c | | | | | | | | | | | | | | | |
| EUPHORBIACEAE | | | | | | | | | | | | | | | | | |
| *Hieronyma guatemalensis* | | | | | | | | | | | | | | | | | |
| [c] *Sapium oligoneuron* | | c | c | | | u | | o | | o | c | | c | | o | c | c |
| RHAMNACEAE | | | | | | | | | | | | | | | | | |
| [d] *Colubrina celtidifolia* | | | | | | | o | c | | | | | | | | | |
| VITACEAE | | | | | | | | | | | | | | | | | |
| sp. A | | | | | o | | | | | | | | | | | | |
| ERYTHROXYLACEAE | | | | | | | | | | | | | | | | | |
| *Erythroxylon amplum* | | | | | | | | o | | | | | | | | | |
| MALPIGHIACEAE | | | | | | | | | | | | | | | | | |
| [d] *Bunchosia pilosa* | | | | | | | | o | | | | | | | | | |
| *B.* sp. A | | | | | | | | c | | | | | | | | | |
| SAPINDACEAE | | | | | | | | | | | | | | | | | |
| [c] *Cupania glabra* | | | | | | | | c | | | | | c | | | c | c |
| [d] *Matayba apetala* | | | | | | | | c | | | | | c | | | | |
| *Paullinia* sp. A | | | | | | | | | | | | | | | | | |
| SIMAROUBACEAE | | | | | | | | | | | | | | | | | |
| *Picramnia carpinterae* | | | | | | | | o | | | | | | | | | |
| MELIACEAE | | | | | | | | | | | | | | | | | |
| [c] *Guarea glabra* | | | | | | | | o | | c | | | o | | | | |
| *G. tonduzii* | | | | | | | | c | | | | | | | | | |
| *G. tuisiana* | c | | | | | | | c | | | | | | | | | |
| *Trichilia havanensis* | | | | | | | | | | | | o | | | | | |
| RUTACEAE | | | | | | | | | | | | | | | | | |
| *Mappia racemosa* | | | | o | | | | c | | | | | | | | | |
| *M.* sp. A | | | | o | | | | | | | | | | | | | |
| *Zanthoxylum culantrillo* | | | | | | | | c | | | | | | | ? | | ? |

TABLE 2. *(Extended)*.

| Bird species[a] | | | | | | | | | | | | | | | | | | | | | | | |
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TABLE 2. *(Continued).*

| Plant species | Bird species[a] | | | | | | | | | | | | | | | | |
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| | BG | BP | RP | RQ | OT | BM | PB | ET | KT | GW | FW | LM | MT | TB | SF | BF | CF |
| ARALIACEAE | | | | | | | | | | | | | | | | | |
| [c] *Dendropanax arboreus* | | | | u | | | | c | | | | | | | | | |
| *D. gonatopodus* | | | | | | | o | | | | | | | | | | |
| [d] *D.* sp. FL | | | | | | | o | c | | | | | | | | | |
| *D. querceti* | | | | | | | | | | | | | | | | | |
| *Schefflera robusta* | | | | | | | | | | | | | | | | | |
| *Didymopanax pittieri* | | | | | | | o | o | | | | | | | | | |
| [c] *Oreopanax oerstedianum* | | | | | | | o | c | | c | c | c | | | u | | |
| *O. xalapensis* | | | | | | | | o | | | | | | | | | |
| *O.* sp. (KGM 82-90-2) | | | | | | | | | | | | | | | | | |
| Subclass Asteridae | | | | | | | | | | | | | | | | | |
| APOCYNACEAE | | | | | | | | | | | | | | | | | |
| [d] *Stemmadenia glabra* | | | | | | | | | | o | | | | | | | |
| *Tabernaemontana* sp. A | | | | | | | | | | | | o | | | | | |
| SOLANACEAE | | | | | | | | | | | | | | | | | |
| [c] *Acnistus arborescens* | | c | o | | o | o | | c | | o | c | c | c | | | c | c |
| [d] *Cestrum megalophyllum* | | | | | | | | c | | | | c | | | | | |
| [d] *C. racemosum* | | | | | | | | c | | | | c | | | | | |
| *C.* sp. A | | | | | | | | o | | | | | | | | | |
| [d] *Lycianthes multiflora* | | | | | | | c | c | | | | o | | | | | |
| [d] *L. synanthera* | | | | | | | | c | | | | | | | | | |
| [d] *Solanum cordovense* | | | | | o | o | | c | | | | c | | | | | |
| *S. hispidum* | | | | | | | | o | | | | | | | | | |
| [d] *S. nudum* | | | | | | | | c | | | | | o | | | | |
| [c] *S. umbellatum* | | | | | | | | c | | | | | | | | | |
| [d] *Witheringia solanacea* | | | | | | | o | u | | | | c | | | | | |
| *W. coccoloboides* | | | | | | | u | | | | | | | | | | |
| *W. maculata* | | | | | | | o | | | | | | | | | | |
| *W.* sp. A | | | | | | | | | | | | | | | | | |
| [c] liana sp. A | | | | | | | | c | | | | | | | | | |
| BORAGINACEAE | | | | | | | | | | | | | | | | | |
| [d] *Tournefortia glabra* | | | | | | | | o | | | | | | | | | |
| VERBENACEAE | | | | | | | | | | | | | | | | | |
| [c] *Citharexylum integerrimum* | | c | c | o | | u | | c | | | | c | | | | o | |
| [c] *C. macradenium* | c | c | | c | | | | c | | | | | | c | | | |
| GESNERIACEAE | | | | | | | | | | | | | | | | | |
| *Alloplectus tetragonus* | | | | | | | | | | | | | | | | | |
| *Besleria formosa* | | | | | | | | | | | | c | | | | | |
| *B. triflora* | | | | | | | | | | | | | | | | | |
| *B.* sp. A | | | | | | | o | | | | | | | | | | |
| *Drymonia conchocalyx* | | | | | | | | | | | | | | | | | |
| *D. rubra* | | | | | | | | | | | | | | | | | |
| CAMPANULACEAE | | | | | | | | | | | | | | | | | |
| *Burmeistera* sp. A | | | | | | | | | | | | | | | | | |
| RUBIACEAE | | | | | | | | | | | | | | | | | |
| *Cephaelis elata* | | | | | | | u | c | | | | | | | | | |
| *Chione costaricensis* | | | | u | u | | | o | | | | | | | | | |
| *Coussarea austin-smithii* | | | | o | u | | | u | | | | | | | | | |
| *C.* sp. A | | | | | u | | | | | | | | | | | | |
| *Faramea quercetorum* | | | | | | | | | | | | o | | | | | |
| [c] *Guettarda poasana* | c | | | u | | | c | c | | | | | | | | | |
| *Gonzalagunia rosea* | | | | | | | u | | | | | | | | | | |
| *Hamelia patens* | | | | | | | | | | | | c | | | | | |
| *Hoffmannia* sp. A | | | | | | | | o | | | | | | | | | |
| *H.* sp. RL | | | | | | | | | | | | | | | | | |

TABLE 2. *(Extended).*

| Bird species[a] | | | | | | | | | | | | | | | | | | | | | | | |
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| DF | YE | ME | OF | BJ | BS | WR | CR | MR | ST | BY | SD | NO | GC | YT | TT | CT | GT | UT | CB | RG | WS | YF | Total[b] |
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| Plant species | Bird species[a] | | | | | | | | | | | | | | | | |
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| | BG | BP | RP | RQ | OT | BM | PB | ET | KT | GW | FW | LM | MT | TB | SF | BF | CF |
| *H.* sp. RF | | | | | | | | | | | | | | | | | |
| *Palicourea galeottiana* | | | | | | | | | | | | c | | | | | |
| *P.* sp. YY | | | | | | | | | | | | | | | | | |
| *Psychotria acuminata* | | | | | | | | o | | | | c | | | | | |
| *P. parasitica* | | | | | | | | | | | | | | | | | |
| *P.* sp. BO | | | | | | | | o | | | | | | | | | |
| *P.* sp. LP | | | | o | | | | | | | | c | | | | | |
| *P.* sp. WB | | | | | | | | | | | | | | | | | |
| CAPRIFOLIACEAE | | | | | | | | | | | | | | | | | |
| [d] *Viburnum costaricanum* | | | | | | | | o | | | | c | | | | o | c |
| ASTERACEAE (COMPOSITAE) | | | | | | | | | | | | | | | | | |
| [d] *Clibadium* sp. A | | | | | | | c | o | | | | | | | | | |
| [d] *C.* sp. B | | | | | | | c | | | | | | | | | | |
| Subclass Arecidae | | | | | | | | | | | | | | | | | |
| ARECACEAE (PALMAE) | | | | | | | | | | | | | | | | | |
| [c] *Chamaedorea* sp. A | c | | | | | | | u | | | | | | | | | |
| ARACEAE | | | | | | | | | | | | | | | | | |
| *Anthurium* sp. A | | | | o | | | | | | | | | | | | | |
| *A.* sp. B | | | | | | | | | | | | o | | | | | |
| *A.* sp. C | | | | | | | | | | | | o | | | | | |
| Subclass Commelinidae | | | | | | | | | | | | | | | | | |
| COMMELINACEAE | | | | | | | | | | | | | | | | | |
| *Campelia zanonia* | | | | | | | | | | | | u | | | | | |
| POACEAE (GRAMINAE) | | | | | | | | | | | | | | | | | |
| *Lasiacis* sp. A | | | | | | | | | | | | o | | | | | |
| Subclass Liliidae | | | | | | | | | | | | | | | | | |
| SMILACACEAE | | | | | | | | | | | | | | | | | |
| *Smilax* sp. A | | | | | | | | o | | | | | | | | | |
| Miscellaneous species | | | | | | | | | | | | | | | | | |
| Epiphyte | | | | | | | | o | o | | | | | | | | |
| Number of species of fruits eaten | 26 | 11 | 4 | 38 | 14 | 9 | 30 | 95 | 16 | 7 | 6 | 37 | 14 | 29 | 6 | 10 | 6 |

[a] Two-letter codes for bird species are defined in Table 1.
[b] Totals for bird species feeding on fruits include the records in Table 3.
[c] >2 h observation of common sp. in appropriate habitat plus repeated (≥10) censuses.
[d] <2 h observation of common sp. in appropriate habitat but ≥10 censuses of plants with ripe fruit.
c = commonly observed.
u = uncommonly observed.
o = occasionally (rarely) observed.

For example, the Lauraceae and the birds that feed on their fruits are well known, whereas the Rubiaceae and birds associated with understory shrubs are generally poorly known. If we rank plant species by the amount of time they were observed (miscellaneous observations only; fewer than 10 censuses or less than 2 hours of observations; or at least 10 censuses plus 2 or more hours of observation), there is a strong positive correlation between research effort and the number of bird species seen feeding on the fruits of a particular species (Spearman Rank Correlation: $r_s = 0.42$; $P < 0.001$; $N = 148$ spp.; all statistical tests are non-parametric and are described in Siegel, 1956; cf. Kantak 1979). These results imply more of a bias than actually exists because we tried to allocate more research effort to plant species already known (on the basis of independent evidence) to be important in birds' diets.

TABLE 2. *(Extended).*

| Bird species[a] | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DF | YE | ME | OF | BJ | BS | WR | CR | MR | ST | BY | SD | NO | GC | YT | TT | CT | GT | UT | CB | RG | WS | YF | Total[b] |
| | | | | | c | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | c | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 2 |
| | | | | | c | | | | | | | | | | | | | | c | | | | 2 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 2 |
| | | | | | o | | | | | | | | | | | | | | | | | | 1 |
| | c | o | | | | | | o | o | | | | | | | | | | | | | | 8 |
| | | | | | u | | | | | c | | | | | | | | | | | | | 4 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 2 |
| | | | | | | | | | | | | | | | | | | | o | | | | 2 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | | | | | | | | | | | | o | | | | | | | | | | | 3 |
| 8 | 4 | 20 | 9 | 13 | 51 | 12 | 10 | 44 | 13 | 13 | 4 | 4 | 14 | 7 | 4 | 13 | 6 | 4 | 29 | 4 | 6 | 7 | 709 |

In other words, many plant species monitored only haphazardly were apparently ignored by birds as well: fruits were not fed to nestlings, seeds failed to appear in seed traps, etc. (cf. Wheelwright 1983). Among 15 species in the Lauraceae, there was no correlation between research effort (4–38 hours of observation/tree species) and number of bird species observed ($P > 0.10$; Wheelwright 1985).

A related problem is that of unequal abundances of different species of plants or birds. After assigning each plant species to one of four categories (rare, uncommon, common, or abundant, based on population estimates made during censuses), a correlation also exists between commonness of a plant species and number of bird species observed feeding on its fruits (Spearman Rank Correlation: $P < 0.001$ for all species [$r_s = 0.49$, $N = 171$], for those studied in some detail [$r_s = 0.47$, $N = 69$], and for those studied more intensively [$r_s = 0.60$, $N = 42$]; $P < 0.01$ for the Lauraceae [$r_s = 0.63$, $N = 15$]). Nevertheless, the fruits of rare plants seldom comprised a major portion of birds' diets, as judged by seed-trapping and recovering fecal samples. Likewise, rare birds are probably less important seed dispersers for most plants than common birds, all else being equal (although see Wheelwright and Orians 1982).

Our varied techniques contribute a third source of bias, that of unequal sampling of birds' diets. Recovering fecal samples from mist-netted birds and using seed traps

TABLE 3. *Fruit species eaten by birds with fewer than four feeding records.*

| Bird species[a] | Fruit species |
|---|---|
| DP | *Sapium oligoneuron* |
| SP | *Sapium oligoneuron, Citharexylum integerrimum* |
| WD | *Acnistus arborescens* |
| GA | *Prunus annularis, Acnistus aborescens, Citharexylum integerrimum* |
| SC | *Acnistus arborescens, Witheringia coccoloboides* |
| RB | *Ocotea tonduzii* |
| SW | *Acnistus arborescens* |
| FP | *Conostegia bernouliana* |
| CD | *Rubus rosaefolia* |
| TK | *Ocotea tonduzii, Colubrina celtidifolia, Acnistus arborescens* |
| GF | *Conostegia bernouliana, Sapium oligoneuron* |
| YC | *Chusquea* sp. A (Poaceae) |
| RN | *Miconia* sp. A |
| BN | *Ossaea micrantha* |
| ON | *Urera elata, Rubus rosaefolia, Citharexylum integerrimum* |
| SV | Melastomataceae sp. NC, *Cupania glabra* |
| YV | *Bocconia frutescens, Acnistus arborescens, Citharexylum integerrimum* |
| BV | *Hampea appendiculata* |
| RH | *Trema micrantha, Stemmadenia glabra, Acnistus arborescens* |
| CO | *Acnistus arborescens, Solanum nudum* |
| BC | *Acnistus arborescens* |
| PT | *Cecropia obtusifolia* |
| HT | *Solanum umbellatum* |
| SB | *Rubus rosaefolia, Miconia* sp. A., *Oreopanax oerstedianum* |
| TS | *Rubus rosaefolia, Acnistus arborescens* |
| GS | *Hampea appendiculata, Acnistus arborescens* |
| YG | *Acnistus arborescens* |
| CC | *Citharexylum integerrimum, Burmeistera* sp. A |
| RS | *Acnistus arborescens, Citharexylum integerrimum* |
| YH | *Miconia* sp. A, *Witheringia solanaceae* |

[a] Two-letter codes for bird species are defined in Table 1.

appear to be the most effective means of obtaining representative diet samples. Consequently, the diets of bird species for which we could use such techniques (*e.g.*, *Myadestes melanops, Phainoptila melanoxantha, Procnias tricarunculata, Chiroxiphia linearis*) are much better known than those of vagrants (*e.g.*, *Eubucco bourcierii*) or migrants (*e.g.*, *Piranga rubra*). The limitations of different sampling techniques probably explain the narrow fruit diets of the latter two groups.

Despite these limitations, it seems worthwhile to present the information on fruit-eating birds that exists for one species-rich tropical forest, Monteverde, especially given the paucity of community-wide studies in other tropical forests (Snow 1981). The breadth of our data base may allow insights into diet choice by birds and "disperser choice" by plants that could not have been gained by narrower, more systematic studies.

The physical characteristics of the fruits of plant species studied (excluding the bulky fruits of the Lauraceae) do not differ significantly from those of co-occurring fruits that share the general syndrome of bird-dispersal (odorless, persistent, juicy, often brightly colored: see van der Pijl 1972; Janson 1983) but for which we have no feeding records (Mann Whitney $U$ test: $P > 0.05$ for each characteristic; $N = 183$ spp.). Therefore, our focal plant species probably represent an unbiased sample of fruits of bird-dispersed plants at Monteverde.

## RESULTS AND DISCUSSION

Snow's (1981) global survey of published feeding records for tropical fruit-eating birds listed the fruits of 420 genera in 100 plant families. We have taken a different but complementary perspective by examining a smaller geographical area in greater detail. At least 70 bird species of the lower montane forests of Monteverde, Costa Rica feed on fruits (Table 1). Fruit-eating birds at Monteverde represent at least 19 families and seven orders (Table 1). Nine of the bird species were studied in detail and their feeding habits are believed to be well known. Seventeen other bird species were studied less systematically but were commonly observed (Table 2). The diets of the remaining bird species are known only from incidental observations (Table 3).

We recorded an average of 10.1 fruit species eaten per bird species, or a total of 709 feeding records (Tables 2 and 3). Table 4 describes the physical characteristics of the fruits eaten by birds. Eighty-nine plant genera in 52 families are represented, including 30 genera and seven families whose fruits are eaten by birds but which are not mentioned by Snow (1981), plus another nine genera previously recorded by Snow only for the Old World tropics (Tables 2 and 3). Plant families are arranged in Table 2 according to phylogenetic order following Cronquist (1981) in order to illustrate possible coevolved relationships at higher taxonomic levels (order, subclass). Few researchers presently expect the evolution of tight, one-to-one mutualisms between individual species of plants and fruit-eating birds (Snow 1981, Howe and Vande Kerckhove 1981, Thompson 1982, Wheelwright and Orians 1982). Instead, they anticipate more general relationships, such as the mutual dependence of birds and a guild of fruit species. For example, birds in the genera *Ptilonopus, Ducula* (Crome 1975), *Procnias* (Snow 1973), and *Pharomachrus* (Wheelwright 1983) feed heavily on fruits of the Lauraceae as a group, but are not restricted to any particular species.

Unlike Snow (1981), we have not classified birds as specialized or unspecialized. No such clear distinctions appear in our data (Table 2). To assign birds to a particular category, one would need to know more about the relative importance of different fruits or alternative foods in the diet. Lacking such information, we have attempted instead to estimate the importance of a given plant species to a bird species by noting how commonly birds were observed feeding on its fruits (Table 2). Because plant and bird species differ in their conspicuousness, commonness, and suitability for different sampling techniques, broad conclusions, even from a single site, should be made with some caution. Comparisons are best made within groups in which such confounding variables have been controlled to some degree. Therefore, we have distinguished the bird and plant species that were thoroughly studied from others studied only casually (Table 2). The bird species listed for well-studied plants (42 plant species, designated by "c" in Table 2) are responsible for an estimated 95 percent (or more) of fruits removed by birds. Those recorded at moderately well-studied plants (27 plant species, designated by "d") probably contribute a majority of fruit removal by birds. Bird species recorded at the remaining (102) plant species remove an unknown proportion of fruits.

For many (36.9%) plant species, we have feeding records involving only a single bird species. For about half of the species, we have records involving fewer than three bird species. For only 8.9 percent of the plant species did we observe more than 10 bird species. In most cases, the observation of a small number of bird species probably reflects the rarity or inconspicuousness of the plant species, or its infrequent use by birds, rather than a specialized or coevolved relationship with a small number of seed dispersers. A perplexing exception is *Solanum umbellatum* (Solanaceae), an abundant shrub that produces clusters of yellow fruits relished by two dissimilar bird species—Emerald Toucanets (*Aulacorhynchus prasinus*) and Yellow-throated Euphonias (*Chiroxiphia linearis*) (as well as various bat species: E. Dinerstein, pers. comm.)—but ignored, at least while alternative fruits are available, by almost all other species. We found significant positive correlations between plant size (herb, shrub, or tree) and the number of bird species observed (*Spearman Rank Correlation*: $r_s = 0.40$, $P < 0.001$, $N = 133$ plant species).

Certain plant species attract a disproportionately large number of bird species. Snow (1981) singled out the plant genera *Cecropia, Ficus,* and *Trema,* which are also popular among birds at Monteverde. Other key genera are *Acnistus* (Solanaceae), *Sapium* (Euphorbiaceae), *Cytharexylum* (Verbenaceae), *Hasseltia* (Flacourteaceae), *Conostegia* (Melastomataceae), and *Hampea* (Malvaceae) (Tables 2 and 3). The species in most of these genera are colonizers of disturbed habitats (tree fall gaps, landslides, abandoned pastures) and produce large crops of medium-sized fruits. *Acnistus arborescens,* a common small tree with watery orange berries produced asynchronously, is fed upon heavily by at least 43 bird species (cf. *Dunalia,* Cruz 1981). Other major food sources for birds are the arillate fruits of *Sapium oligoneuron* and *Hampea appendiculata,* which both draw 22 bird species (cf. *Guarea,* Howe and De Steven 1979). *Ocotea tonduzii* (Lauraceae) is unusual among "high investment, high quality" fruits (Table 4) in having its seeds dispersed by at least 18 bird species. It fails to support the predictions of some models (McKey 1975, Howe and Estabrook 1977) because it attracts many species, including generalists such as flycatchers and migrating thrushes. During a four month period, *O. tonduzii* fruits comprised 59.0 percent ($N = 1393$) of the fruits eaten by male Three-wattled Bellbirds (*Procnias tricarunculata*) at five calling perches (Wheelwright unpubl. data) and 63.8 percent ($N = 58$) of those delivered to nestling Resplendent Quetzals (*Pharomachrus mocinno*) at two nests (Wheelwright 1983).

Among plant families, the Lauraceae and Moraceae support particularly large numbers of fruit-eating birds. The Rubiaceae, Melastomataceae, and Solanaceae also include many bird-dispersed species, but with the exception of *Acnistus* they tend to produce small crops fed upon chiefly by understory birds. Nonetheless, they probably constitute a major portion of the diets of understory/subcanopy species such as solitaires and manakins. For example, 26.2 percent of 844 fruits eaten by male Long-tailed Manakins at seven display perches represented eight species in the Solanaceae, 8.9 percent represented three species in the Melastomataceae, and 5.2 percent represented five species in the Rubiaceae (Wheelwright unpubl. data).

Feeding records reflect unequal degrees of frugivory among different groups. Non-passerines accounted for a far greater number of feeding records (Tables 2 and 3) than expected by their number of species (mean number of fruit species eaten/bird species = 14.8; $\chi^2$ Two-Sample Test: $P < 0.001$). Similarly, sub-oscines (versus oscines) and thrushes (versus other passerines) ate a wider than average range of fruit species ($\bar{x} = 10.0$ and 17.1 fruit species/bird species, respectively; $\chi^2$ Two-Sample Tests: $P < 0.05$ and $P < 0.001$, respectively). The same results hold even if fruit records involving the more thoroughly studied Lauraceae are excluded. Note that these and other results should be viewed in the context of sampling biases, discussed above, although they are consistent with widely accepted impressions of the food habits of neotropical birds (*e.g.,* Skutch 1967).

Bird species that depend mainly on fruits for food are no more likely to be polygamous or sexually dimorphic in plumage than birds that eat little or no fruit, in spite of expectations to the contrary (Snow 1971). We divided bird species into four groups based on the number of fruit species recorded in their diet (0, 1–9, 10–19, 20 or more; Tables 2 and 3). Of course, some more direct measure of the importance of fruits would be preferable to number of species eaten. Such information is difficult to get for

TABLE 4. *Characteristics of fruits eaten by birds at Monteverde, Costa Rica.*

| Family | Species | Wet fruit diam. (cm) | Wet fruit wt. (g) | Fruit display[a] | Percent water | Per-cent sug-ar | Wet seed wt/ wet fruit wt | % N | % Crude fat | % TNC[b] |
|---|---|---|---|---|---|---|---|---|---|---|
| Annonaceae | *Guatteria consanguinea* | 1.7 | 2.70 | Black & red | 86 | 5 | 0.09 | 1.1 | 3.3 | 21.0 |
| Apocynaceae | *Stemmadenia glabra* | 0.6 | 0.13 | Black & orange | — | — | 0.69 | — | — | — |
| | *Tabernaemontana* sp. A | 0.8 | 0.25 | Black & orange | — | 12 | 0.48 | — | — | — |
| Aquifoliaceae | *Ilex lamprophylla* | 0.5 | 0.07 | Red | — | — | 0.29 | — | — | — |
| Aracaceae | *Chamaedorea* sp. A | 1.0 | 0.55 | Black & orange | — | 12 | 0.67 | — | — | — |
| Araceae | *Anthurium* sp. A | 0.6 | 0.13 | Red | — | 5 | 0.08 | — | — | — |
| | *A.* sp. B | 0.8 | 0.52 | Red & pink | — | 4 | 0.35 | — | — | — |
| | *A.* sp. C | 0.9 | 0.49 | Orange | — | 9 | 0.12 | — | — | — |
| Araliaceae | *Dendropanax arboreus* | 0.7 | 0.20 | Black & white | — | — | 0.05 | — | — | — |
| | *D. gonatopodus* | 0.7 | 0.14 | Black & white | — | 8 | 0.43 | — | — | — |
| | *D.* sp. FL | 0.5 | 0.08 | Black & white | — | 22 | 0.13 | — | — | — |
| | *Didymopanax pittieri* | — | — | Black & white | — | — | — | — | — | — |
| | *Oreopanax oerstedianum* | 0.6 | 0.10 | Black & white | — | 31 | 0.20 | — | — | — |
| | *O. xalapensis* | 0.7 | 0.15 | Black & white | — | 13 | 0.27 | — | — | — |
| Asteraceae | *Clibadium* sp. A | 1.0 | 0.59 | Black | — | 4 | 0.05 | — | — | — |
| | *C.* sp. B | 0.5 | 0.06 | Black | — | 6 | 0.17 | — | — | — |
| Boraginaceae | *Tournefortia glabra* | 0.7 | 0.16 | White | — | 6 | 0.25 | — | — | — |
| Campanulaceae | *Burmeistera* sp. A | 0.8 | 0.32 | Red | — | 5 | 0.06 | — | — | — |
| Caprifoliaceae | *Viburnum costaricensis* | 0.6 | 0.12 | Black | — | 17 | 0.42 | — | — | — |
| Cecropiaceae | *Cecropia obtusifolia* | — | — | Green | — | — | — | — | — | — |
| Celastraceae | Sp. A | 2.0 | 3.50 | Red & orange | — | — | 0.29 | — | — | — |
| | *Perrottetia longistylis* | 0.6 | — | Red | — | — | — | — | — | — |
| | *Maytenus* sp. A | 0.6 | — | Black & white | — | — | — | — | — | — |
| Clusiaceae | *Clusia elata* | 0.3 | 0.05 | Red | — | 5 | 0.60 | — | — | — |
| Commelinaceae | *Campelia zanonia* | 0.8 | 1.20 | Black | — | 1 | 0.08 | — | — | — |
| Cucurbitaceae | Sp. A | 1.3 | 1.65 | Black | — | 6 | 0.21 | — | — | — |
| Ericaceae | *Cavendishia melastomoides* | 1.1 | 0.65 | Blue & white | — | 14 | 0.05 | — | — | — |
| | *C.* sp. A | 1.0 | 0.42 | Red & pink | — | 3 | 0.05 | — | — | — |
| Erythroxylaceae | *Erythroxylon amplum* | 0.6 | 0.16 | Red & yellow | — | 21 | 0.44 | — | — | — |
| Euphorbiaceae | *Sapium oligoneuron* | 0.6 | 0.07 | Red | — | — | 0.86 | — | — | — |
| Flacourtiaceae | *Casearia sylvestris* | 0.8 | 0.17 | Orange & yellow | — | 6 | 0.53 | — | — | — |
| | *Hasseltia floribunda* | 0.8 | 0.20 | Dark red & red | 90 | 4 | 0.20 | 1.3 | 0.9 | 37.8 |
| | *Xylosma chloranthum* | 1.1 | 0.77 | Black & red | — | 12 | 0.23 | — | — | — |
| | *X. flexuosa* | 0.9 | 0.40 | Red | — | 15 | 0.15 | — | — | — |
| | *X. intermedium* | 0.6 | 0.15 | Black | — | 8 | 0.13 | — | — | — |
| Gesneriaceae | *Beslaria formosa* | 0.8 | 0.31 | Orange | — | 6 | 0.05 | — | — | — |
| Lauraceae | *Beilschmiedia* sp. BC | 2.2 | 12.89 | Black | 69 | — | 0.48 | 1.1 | 11.6 | 10.2 |
| | *B. costaricensis* | 2.3 | 12.42 | Black | 76 | — | 0.63 | 1.3 | 11.2 | 3.4 |
| | *B.* sp. BL | 2.5 | 15.19 | Black | 64 | — | 0.52 | — | — | — |
| | *Nectandra* sp. NC | 1.0 | 1.08 | Black & red | 65 | — | 0.40 | — | — | — |
| | *N. davidsoniana* | 1.7 | 3.25 | Black & red | 77 | 9 | 0.57 | 1.2 | 25.3 | 11.0 |
| | *N. gentlei* | 1.2 | 0.98 | Black | 63 | — | 0.49 | 1.6 | 36.1 | 9.0 |
| | *N. hypoglauca* | 1.8 | 5.50 | Black & red | 67 | — | 0.52 | 1.5 | 32.2 | 17.9 |
| | *N. salicina* | 1.9 | 7.42 | Black & red | 69 | 10 | 0.52 | 1.3 | 37.3 | 20.1 |
| | *N.* sp. NV | 1.7 | 4.03 | Black & red | 67 | — | 0.52 | — | — | — |
| | *Ocotea austinii* | 1.1 | 1.31 | Black & red | 62 | — | 0.48 | 1.1 | 45.2 | 8.7 |
| | *O. bernouliana* | 1.8 | 6.62 | Black & red | 86 | 6 | 0.58 | 2.3 | 5.8 | 7.9 |
| | *O.* sp. FL | 2.2 | 9.28 | Black & red | 84 | 3 | 0.55 | 1.9 | 23.5 | 7.4 |
| | *O. klotzschiana* | 1.8 | 5.98 | Black & red | 86 | — | 0.50 | 3.2 | 18.3 | 6.5 |
| | *O.* sp. K2 | 2.0 | 7.43 | Black & red | 78 | — | 0.54 | 2.4 | 26.9 | 17.0 |
| | *O.* sp. RP | 1.2 | 1.37 | Black & red | 75 | — | 0.55 | 2.8 | 17.3 | 3.6 |
| | *O. tonduzii* | 1.2 | 1.34 | Black & red | 66 | 14 | 0.43 | 1.0 | 29.4 | 16.7 |
| | *O. wachenheimii* | 1.7 | 2.94 | Black | 76 | 12 | 0.56 | 1.4 | 31.1 | 17.7 |
| | *Persea* sp. RP | 0.8 | 0.29 | Blue | 52 | — | 0.52 | — | — | — |
| | *P. veraguensis* | 1.1 | 0.67 | Blue | 58 | — | 0.67 | — | — | — |
| | *Phoebe neurophylla* | 1.3 | 1.62 | Black & red | 68 | — | 0.36 | 1.1 | — | 10.2 |
| | *P. mexicana* | 1.2 | 1.38 | Black & red | 68 | 7 | 0.50 | 1.2 | 28.0 | 9.0 |

TABLE 4. *(Continued).*

| Family | Species | Wet fruit diam. (cm) | Wet fruit wt. (g) | Fruit display[a] | Percent water | Percent sugar | Wet seed wt/wet fruit wt | % N | % Crude fat | % TNC[b] |
|---|---|---|---|---|---|---|---|---|---|---|
| Liliaceae | *Smilax* sp. A | 1.1 | 0.57 | Red & orange | — | 3 | 0.30 | — | — | — |
| Loranthaceae | Sp. A | 0.5 | — | Black & orange | — | — | — | — | — | — |
| | Sp. B | 0.5 | 0.05 | Brown | — | 12 | 0.20 | — | — | — |
| | *Gaiadendron punctatum* | 0.3 | 0.02 | Yellow | — | — | 0.50 | — | — | — |
| Malpighiaceae | *Bunchosia* sp. A | 2.7 | 9.20 | Green | — | — | 0.23 | — | — | — |
| | *B. pilosa* | 1.8 | 2.17 | Red & orange | — | — | 0.33 | — | — | — |
| Malvaceae | *Hampea appendiculata* | 1.1 | 0.50 | Black & white | 56 | — | 0.65 | 0.7 | 0.3 | 35.2 |
| | *Malvaviscus arboreus* | 1.3 | 0.30 | Red | 91 | 5 | 0.10 | — | — | — |
| Marcgraviaceae | *Marcgravia brownei* | 0.9 | 0.29 | Red & yellow | — | 17 | 0.10 | — | — | — |
| Melastomataceae | *Blakea* sp. A | 0.8 | — | Red | — | 6 | — | — | — | — |
| | *Conostegia bernouliana* | 1.1 | — | Black | — | 10 | — | — | — | — |
| | *C. xalapensis* | 0.9 | 0.30 | Black | — | — | 0.05 | — | — | — |
| | *Ossaea* sp. A | 0.6 | 0.09 | White | — | 7 | 0.05 | — | — | — |
| | *O. micrantha* | 0.5 | — | Black & blue | — | — | — | — | — | — |
| Meliaceae | *Guarea tonduzii* | 0.8 | 0.48 | Red & white | — | — | 0.94 | — | — | — |
| | *G. tuisiana* | 2.2 | 7.45 | Red & white | — | 18 | 0.85 | — | — | — |
| | *G. glabra* | — | — | Red & white | — | — | — | — | — | — |
| | *Trichilia havanensis* | 0.6 | 0.11 | Red | — | — | 0.64 | — | — | — |
| Monimiaceae | *Siparuna* sp. A | 0.4 | 0.03 | Red & blue | — | — | 0.67 | — | — | — |
| Moraceae | *Ficus pertusa* | 1.0 | 1.00 | Dark red & red | — | 8 | 0.08 | — | — | — |
| | *F. tuerckheimii* | 1.7 | 2.60 | Red | — | 6 | 0.08 | — | — | — |
| | *Trophis mexicana* | 0.8 | 0.21 | Red | — | 14 | 0.19 | — | — | — |
| Myrsinaceae | *Ardisia compressa* | 0.9 | 0.37 | Black & red | — | 3 | 0.24 | — | — | — |
| | *A. palmana* | 1.3 | 0.21 | Black & red | 88 | 8 | 0.24 | 0.6 | 2.6 | 30.6 |
| | *Rapanea myricoides* | 0.4 | 0.01 | Black | — | — | — | — | — | — |
| Myrtaceae | *Eugenia* sp. A | 1.2 | 0.76 | Black & red | — | 7 | 0.36 | — | — | — |
| | *E.* sp. B | 1.7 | 4.82 | Red & orange | 80 | 12 | 0.48 | 0.7 | 1.7 | 18.0 |
| Nyctaginaceae | *Neea amplifolia* | 1.2 | 1.19 | Dark red & red | — | 7 | 0.20 | — | — | — |
| | *Torrubia costaricensis* | 0.7 | 0.28 | Dark red & red | — | 13 | 0.36 | — | — | — |
| Papaveraceae | *Bocconia frutescens* | 0.3 | 0.25 | Black & red & yellow | — | 20 | 0.72 | — | — | — |
| Phytolaccaceae | *Phytolacca rivinoides* | 0.8 | 0.23 | Black & red | — | 9 | 0.17 | — | — | — |
| | *P.* sp. A | 0.7 | 0.12 | Black & red | — | — | 1.00 | — | — | — |
| Piperaceae | *Piper auritum* | — | — | Green | — | — | — | — | — | — |
| Poaceae | *Lasiacis* | — | — | Black | — | — | — | — | — | — |
| Rhamnaceae | *Colubrina* | — | — | Orange | — | — | — | — | — | — |
| Rosaceae | *Prunus cornifolia* | 1.7 | 2.78 | Black & red | 76 | 18 | 0.46 | 0.8 | 0.5 | 38.0 |
| | *P.* sp. A | 1.5 | 1.40 | Black & red | — | 12 | 0.29 | — | — | — |
| | *P. annularis* | 1.5 | 2.24 | Black & red | — | 12 | 0.24 | — | — | — |
| | *Rubus rosaefolia* | 1.7 | — | Black | 77 | 8 | 0.37 | — | — | — |
| Rubiaceae | *Chione costaricensis* | 1.0 | — | Red | — | — | — | — | — | — |
| | *Coussaria austin-smithii* | 1.7 | 1.90 | Black & blue | 94 | — | 0.42 | 2.1 | — | — |
| | *C.* sp. A | 1.4 | — | Black & blue | — | — | — | — | — | — |
| | *Faramea quercetorum* | 1.1 | 0.90 | Blue | — | 2 | 0.46 | — | — | — |
| | *Guettarda poassana* | 0.8 | — | Black & blue | — | — | — | — | — | — |
| | *Hamelia patens* | 0.9 | 0.30 | Black & red | — | 10 | 0.03 | — | — | — |
| | *Hoffmannia* sp. A | 0.9 | 0.29 | Black & red | — | 2 | 0.03 | — | — | — |
| | *Palacourea galeottiana* | 0.8 | 0.57 | Black | — | 4 | 0.07 | — | — | — |
| | *Psychotria acuminata* | 0.9 | 0.38 | Black & yellow | — | — | 0.26 | — | — | — |
| | *P.* sp. BO | 1.1 | 0.71 | Black & blue | — | 3 | 0.11 | — | — | — |
| | *P.* sp. LP | 0.8 | 0.29 | Red & yellow | — | 5 | 0.07 | — | — | — |
| | *P.* sp. C | 1.0 | 0.50 | Red & orange | — | 4 | 0.18 | — | — | — |
| Rutaceae | *Mappia racemosa* | 1.7 | 5.90 | Black | 77 | 8 | 0.37 | 2.0 | 1.2 | — |
| | *M.* sp. A | 0.5 | — | Brown | — | — | — | — | — | — |
| | *Zanthoxylum* sp. A | 0.4 | 0.03 | Black | — | — | 1.00 | — | — | — |
| Sabiaceae | *Meliosma idiopoda* | 1.1 | 1.10 | Yellow & white | — | — | 0.09 | — | — | — |
| Sapindaceae | *Cupania glabra* | 0.8 | — | Red & orange | — | — | — | — | — | — |

TABLE 4. *(Continued).*

| Family | Species | Wet fruit diam. (cm) | Wet fruit wt. (g) | Fruit display[a] | Percent water | Percent sugar | Wet seed wt/ wet fruit wt | % N | % Crude fat | % TNC[b] |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Matayba apetala* | 0.8 | — | Black & orange | — | — | — | — | — | — |
| | *Paullinia* sp. A | 0.9 | 0.25 | Black & white & red | — | 24 | 0.60 | — | — | — |
| Simaroubaceae | *Picramnia carpenterae* | 1.1 | — | Black & red | — | — | — | — | — | — |
| Solanaceae | *Acnistus arborescens* | 0.8 | 0.24 | Orange | — | 13 | 0.08 | — | — | — |
| | *Cestrum* sp. A | 0.8 | 0.22 | Black | — | 10 | 0.14 | — | — | — |
| | *C. megaphyllum* | 0.8 | 0.53 | Black & blue | — | 7 | 0.21 | — | — | — |
| | *C. racemosa* | 0.7 | 0.48 | Black & blue | — | 7 | 0.06 | — | — | — |
| | *Lysianthes multiflora* | 1.3 | 1.15 | Red | 89 | 9 | 0.13 | 2.1 | 1.3 | 15.6 |
| | *L. synanthera* | 0.9 | 0.40 | Yellow | — | — | 0.13 | — | — | — |
| | *Solanum cordovense* | 0.9 | 0.52 | Black | — | 11 | 0.08 | — | — | — |
| | *S. nudum* | 1.2 | 1.31 | Yellow | — | 12 | 0.20 | — | — | — |
| | *S. umbellatum* | 1.3 | 1.11 | Yellow | — | 11 | 0.19 | — | — | — |
| | *Witheringia solanaceae* | 1.2 | 0.71 | Orange | — | 5 | 0.17 | — | — | — |
| | *W. coccoloboides* | 1.0 | 0.58 | Orange | 90 | — | 0.09 | — | — | — |
| | *W.* sp. A | 1.0 | 0.64 | Orange | — | 4 | 0.05 | — | — | — |
| | *W. maculata* | — | — | Red | — | — | — | — | — | — |
| Symplocaceae | *Symplocos limoncillo* | 1.0 | 0.90 | Blue | — | — | — | — | — | — |
| | *S.* sp. A | 1.9 | 5.26 | Blue | — | 18 | 0.43 | — | — | — |
| | *S.* sp. B | — | — | Blue | — | — | — | — | — | — |
| Theaceae | *Symplocarpon* sp. A | 1.0 | 0.84 | Blue | — | 9 | 0.19 | — | — | — |
| Thymeliaceae | *Daphnopsis* | 0.8 | 0.23 | White | — | 24 | 0.26 | — | — | — |
| Ulmaceae | *Trema micrantha* | 0.4 | 0.02 | Orange | — | 12 | 0.50 | — | — | — |
| Urticaceae | *Urera elata* | 0.3 | — | Red | — | 6 | 0.25 | — | — | — |
| Verbenaceae | *Citharexylum integerrimum* | 0.8 | 0.21 | Black & yellow | — | 20 | 0.33 | 0.8 | 2.0 | 38.1 |
| | *C. macradenium* | 1.1 | 0.70 | Black & orange | 75 | 20 | 0.13 | 0.3 | 2.5 | 38.4 |
| Vitaceae | *Cissus* sp. A | 1.1 | 0.52 | Black | — | 5 | 0.19 | — | — | — |
| Unknown | Epiphyte sp. A | 0.5 | 0.07 | Brown | — | — | 0.14 | — | — | — |

[a] "Fruit display" represents the color of ripe fruits. Species with "simple" displays (e.g., "red" and "black") have green unripe fruits and lack contrastingly colored associated structures (see text).
[b] Total nonstructural carbohydrates.

any bird species, but where it is available, there seems to be a good correspondence between number of fruits eaten and degree of frugivory (cf. Skutch 1967, Table 2). About 10 percent of all Monteverde bird species are polygamous and about 20 percent are sexually dichromatic. These proportions do not differ significantly among categories reflecting degree of frugivory ($\chi^2$ Two-Sample Test: $P > 0.05$). Of ten bird species that feed on 20 or more species of fruits, only two (*Procnias tricarunculata* and *Chiroxiphia linearis*) are polygamous and only three (the same two species plus *Pharomachrus mocinno*) are distinctly sexually dichromatic.

If birds are to be determined as specialized on the basis of the frequency of fruit in their diets (Wheelwright and Orians 1982) and not on the quality of seed dispersal they deliver (Howe and Estabrook 1977) or the characteristics of the fruits they select (Snow 1981), we would add the following genera to Snow's (1981) list: *Chamaepetes, Elaenia, Mionectes, Myadestes, Phainoptila, Chlorophonia,* and *Euphonia*. The evidence is inconclusive that all pigeons in the genus *Columba* are seed predators (Olson and Blum 1968); at Monteverde *C. fasciata* in particular may be effective seed dispersers of many plants with small seeds. Several *Turdus* and *Catharus* species eat fruit almost exclusively during some seasons and could be considered fruit specialists at such times.

Diet choice by birds at Monteverde and its selective influence on the evolution of fruit traits have been analyzed elsewhere (Wheelwright 1985). Therefore, we simply provide summary statistics and many of the original data here. For the fruits in Table 4, the means (and standard deviations) are as follows: weight 1.60 (±2.76) g; diameters 10.5 (±4.9) mm; sucrose equivalents measured by refractometer 9.88 (±6.18) percent; and seed:

fruit ratios 0.32 ($\pm$0.23). A black fruit with contrastingly colored (not black, brown, or green) unripe fruits or associated structures (bracts, pedicels) is the most common fruit display; simple displays of black or red fruits that are green when unripe follow in frequency (Table 4).

## CONCLUSION

When Herrera (1981) set out to compare the quality of temperate and tropical fruits, he could uncover appropriate data for only 15 tropical plant species. Moreover, as he noted, those were hardly a representative sample of tropical fruits. Thirteen of the 15 species (87%) have single-seeded fruits, as opposed to only 113 of 263 species (43%) in the lower montane forests of Monteverde. Seed : fruit ratios and Herrera's (1981) measure of fruit quality depend strongly on seed number, single-seeded fruits having relatively little pulp for a given seed weight (cf. Table 4). The major conclusion of Herrera's paper—that tropical and temperate fruits are equivalent in terms of overall profitability—is not supported when a more representative sample of tropical fruits is used. Monteverde fruits have far lower overall profitabilities ($\bar{x}$ = 1.77, SD = 2.99, $N$ = 13) than either the temperate or tropical samples reported by Herrera (1981) (Mann-Whitney $U$ Test: $P <$ 0.01) once we exclude all but two randomly selected Lauraceae (in order not to bias the sample of fruits in Table 4 for which there is nutritional information towards heavy or oily fruits). Ricklefs (1977), hampered by the same shortage of adequate data, could compare only four plant species from different habitats in his attempt to discriminate groups of bird species feeding at different trees. The problems of sampling from a heterogeneous, inadequate literature continue to plague general surveys and create controversy (cf. Stiles 1980, Herrera 1982, Stiles and White 1982). The data presented here and in Janson (1983) should contribute a more realistic view of the diversity of tropical fruits and the complex choices fruit-eating birds make between them.


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## Notice for the Second International Legume Conference

The Second International Legume Conference, held jointly by the Missouri Botanical Garden and the Royal Botanic Gardens, Kew, will take place on 23–27 June, 1986. Sessions will be held in the Ridgway Center at the Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, USA.

The Conference theme is the Biology of the Leguminosae. The aim of the meeting is to discuss recent advances in our understanding of the biology of legumes, gained from both field and experimental research, and covering both pure and applied points of view. The multidisciplinary approach of the Conference is designed to address a wide variety of research interests and to stimulate discussion among specialists. The working language of the Conference will be English.

Scheduled topics include: life history studies; tree architecture; evolution and biology of inflorescences and pollen; floral organogenesis; ecology; ecological biogeography; pollen-stigma-style interactions; structure and function of legume fruits and seeds; mycorrhizal relationships; cyanogenesis; evolution of symbiotic genes; biological implications of genome evolution; ant-domatia, aphid-legume, tick-legume, and bruchid-legume co-evolution; biological changes induced by domestication; computerized data bases and biological research; international legume data bases.

Participation in the Conference will be limited to 350 persons. If you would like more information or wish to submit a proposal for a poster presentation, please contact Dr. James L. Zarucchi, Legume Conference Coordinator, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, USA.