

DIETS OF UNDERSTORY FRUIT-EATING BIRDS IN COSTA RICA: SEASONALITY AND RESOURCE ABUNDANCE

BETTE A. LOISELLE AND JOHN G. BLAKE

Abstract. Diets of understory fruit-eating birds were examined in five habitats in northeastern Costa Rica. Diets were quantified by analyzing seeds contained in fecal samples collected from mist-netted birds. We show that neotropical understory frugivores partition fruit resources. Six frugivore guilds were identified by Bray-Curtis ordination. Number of species per guild varied from one to seven. Not all guilds were present at each site (young and old second-growth, and primary forest at 50-m, 500-m, and 1000-m elevations). Guild composition was influenced by morphology, fruit display and type, feeding method, and foraging height. Birds differed in preference or avoidance of fruit species; preferences varied seasonally, annually, and among habitats. Birds were more selective in areas with high fruit abundance (second-growth) than in areas with low fruit abundance (forest).

Key Words: Costa Rica; diet; frugivores; fruits; seasonality.

Plants that produce fleshy fruits and birds that consume fruits are important components of many tropical habitats. From 63 to 77% of understory shrubs and trees produce bird-dispersed fruits in Costa Rican evergreen forests (Stiles 1985a) and fruit-eating birds often constitute a large proportion of tropical avifaunas (Stiles 1985a, Blake et al. in press, Karr et al. in press). The few specific studies have revealed that those birds feed on a wide variety of fruits (Snow 1962a, 1962b, Jenkins 1969, Snow and Snow 1971, Worthington 1982). Even so, diets of most understory fruit-eating birds in neotropical habitats are largely unknown.

Many studies of fruit-frugivore interactions have documented what bird species consume fruit and disperse seeds of a particular species or group of plants. A diverse assemblage of bird species visit trees with abundant fruit crops (e.g., Eisenmann 1961, Willis 1966, Leck 1973, Kantak 1979, Howe 1981). From such studies, some researchers (e.g., McKey 1975, Howe and Estabrook 1977) have proposed a specialist-generalist dichotomy, with small understory frugivores feeding opportunistically and large, canopy frugivores specializing on a limited subset of fruits. However, understory birds also can be highly selective in their choice of fruits (Moermond and Denslow 1985).

Here we present data on the diets of understory frugivores to examine how feeding preferences of birds for common fruiting plants vary in relation to fruit abundance and seasonality. Diet information was obtained from birds in five Costa Rican sites that represent different successional and forest elevational stages. We examine whether understory frugivores are generalists or

opportunists, as proposed by previous authors, or selective as suggested by aviary work. Because community-wide fruit production varies among sites, we examine whether and how habitat influences foraging patterns. In habitats with low fruit abundance, understory frugivores likely compete for fruits and partition fruit resources. In areas with high fruit abundance, such as young second-growth, competition for fruits is less. Instead, plants may compete for dispersers. Birds should be more selective in areas with high than low fruit abundance, and if a given fruit species is equally attractive to birds, then feeding preference and diet should overlap broadly.

METHODS

STUDY AREA

The study area was on the Caribbean slope of the Cordillera Central in northeast Costa Rica. Lowland sites were in 5–10 year second-growth, 25–35 year second-growth, and primary (undisturbed) forest at the Estación Biológica La Selva (10°25'N, 84°01'W). We also sampled diets of fruit-eating birds in primary forest at 500-m (10°20'N, 84°04'W) and at 1000-m (10°16'N, 84°05'W) in Parque Nacional Braulio Carrillo, about 15 km and 20 km south of La Selva, respectively.

La Selva receives about 4000 mm rain annually (Hartshorn 1983; Organization for Tropical Studies, unpubl. data). The main dry season lasts from January or February to March or April with a shorter, less pronounced dry season in September and October. Climatological data are not available for the 500-m and 1000-m sites, but annual rainfall probably exceeds 4500 mm at both. During this study, rainfall generally was below the 20-year average and the dry season effectively lasted from January through April. Further descriptions of those sites are in Frankie et al. (1974), Hartshorn (1983), and Pringle et al. (1984).

DATA COLLECTION

Our diet analyses were based primarily on seeds and pulp from feces or regurgitated material (hereafter referred to as "fecal samples") from mist-netted birds. We collected data from January 1985 through April 1986 and from December to mid-April 1987. Samples were collected every 5–6 weeks at each site. Total sampling effort was less at higher sites due to a variety of logistical and weather-related problems. We had not analysed all 1987 data when this paper was written and here include 1987 data from only the youngest site.

We placed all mist-netted birds (except hummingbirds and raptors) in plastic containers lined with filter paper for 5 to 15 min. More than 80% of the birds produced samples; only a few species (e.g., hole nesters such as Wedge-billed Woodcreeper [scientific names of all birds are in Appendix 1]) regularly failed to defecate in containers. We collected 4037 fecal samples; 57% contained fruit pulp, seeds, or both. Using a dissecting microscope, we separated seeds from fecal samples and identified them to species through comparison with a reference collection at La Selva. Some seeds were lumped by genera in our analyses because species could not be distinguished (e.g., *Anthurium*, *Sabicea*, *Clusia*, *Ficus*).

We estimated understory fruit abundance (see also Loiselle [1987]) by counting all fruiting individuals and ripe and unripe fruits in belt transects that paralleled each side of each mist net (50 m²/net). Fruits were sampled at 20 mist nets (1000 m² total sampling area) in each highland area, at 30 mist nets (1500 m² total sampling area) in each second-growth site, and at 54 mist nets (2700 m² total sampling area) in primary forest at La Selva.

DATA ANALYSIS

We used data from all five sites to describe frugivore assemblages in the following analyses. However, because of smaller sample sizes, we did not include our highland sites (500 and 1000-m) in analyses of seasonal or annual variation in fruit use.

Accumulation curves

We plotted cumulative number of fruit species in the diet against sample effort (i.e., number of fecal samples) to construct fruit species accumulation curves. We included all samples (i.e., those containing only insect parts as well as those containing fruit) in the analyses. We fitted accumulation curves to three regression functions: linear (nontransformed), exponential (species/log sample number), and power (log species/log sample number). We used accumulation curves to evaluate sample sizes needed to describe diets of birds and to compare slopes of fruit species accumulation among some bird species.

Multivariate analyses

The original data matrix for each site consisted of the number of times a given fruit species occurred (i.e., at least one seed) in fecal samples for each bird species (bird-species by fruit-species matrix). We simplified the data matrix by combining fruits into 9 to 15 cat-

egories defined by fruit presentation, location, and type, and by seed number and size (Appendix 2). Some species or genera (e.g., *Phytolacca rivinoides* and *Passiflora* sp.) did not readily fit into any category and were treated as separate groups. Furthermore, because species composition and representation of fruiting plants in birds' diets varied among habitats, assignment of fruit variables differed among sites. For example, some fruit variables (e.g., aggregate fruits such as *Piper*) were appropriate at one site only, while others (e.g., fruits of aroids and bromeliads) were lumped or divided depending on sample sizes at each site (Appendix 2). This simplification was necessary because of the relative rarity of many fruit species in bird diets. We further simplified the data matrix by excluding birds that rarely ate fruit or that were under-represented among fecal samples.

We relativized the data by rows (birds) (Greig-Smith 1983:248), so that use of a fruit was expressed as a proportion of total fruit used by that species. This "standardization by the norm" eliminates problems arising from unequal sample sizes. This core set of frugivores was ordinated in fruit-species space for each site using a Euclidean distance measure and Bray-Curtis ordination with variance-regression criterion for axis orientation (Beals 1984). Use of a standardized distance with Bray-Curtis construction of axes eliminates the effects of ecologically ambiguous "joint nonuse" of resources that are emphasized by covariance or correlation values used in construction of principal component axes (E. W. Beals, pers. comm.). Fruit variables were correlated with ordination axes. All multivariate analyses were run on PC-ORD (McCune 1987).

Seasonal and annual use of fruit

We divided our samples into four or five (young second-growth) seasons on the basis of rainfall totals to allow evaluation of both seasonal and annual variation in use of fruit by birds. Abundance of ripe fruit at each lowland site was totalled by season for dominant understory fruiting plants. We used an index developed by Jacobs (1974) to evaluate use of a fruiting species in relation to its availability (feeding preference):

$$D_{fr} = \frac{(r - p)}{(r + p - 2rp)}$$

where D_{fr} is an index of fruit use, r is proportion of that fruit species in the diet, and p is proportion of ripe fruit (available) in the habitat accounted for by that species. We followed Morrison (1982) who categorized this index, which ranges from -1 to $+1$, as follows: D_{fr} of 0 to ± 0.15 = no preference, ± 0.16 to 0.40 = slight preference or avoidance, ± 0.41 to 0.80 = moderate preference or avoidance, and ± 0.81 to 1.00 = strong preference or avoidance. Fruit use was evaluated by comparing observed number of fecal samples that contained that fruit species to that expected from availability of ripe fruit (χ^2 analysis, Zar 1984:40–42). We further analysed seasonal and annual use of fruit species by comparing number of occurrences of a particular fruit in the diet in relation to all other fruit species in the diet (χ^2 analysis).

TABLE 1. NUMBER OF SAMPLES CONTAINING FRUIT, NUMBER OF BIRD SPECIES REPRESENTED IN THOSE SAMPLES, AND NUMBER OF FRUIT SPECIES CONTAINED IN THOSE SAMPLES FOR EACH OF FIVE COSTA RICAN SITES. NUMBER OF FRUIT SPECIES WAS UNDERESTIMATED BECAUSE SPECIES OF SOME GENERA WERE LUMPED (SEE TEXT). DATA FROM YOUNG SECOND-GROWTH WERE COLLECTED FROM 1985–1987; DATA FROM ALL OTHER SITES WERE COLLECTED FROM 1985–1986

Site	Number of fecal samples with fruit	Number of bird species	Number of fruit species
Second-growth:			
young (5–7 year)	1119	57	81
old (25–35 year)	339	27	69
Primary forest:			
lowland	366	21	55
500 m	219	21	55
1000 m	252	22	70

Use of fruit by common fruit-eating birds

We supplemented ordination and feeding preference data by examining diets of some key frugivores in each lowland habitat. We used Kendall's coefficient of concordance (Zar 1984:352–359) to test whether relative use of common fruiting plants found in fecal samples was similar among those birds. We further compared feeding preferences of individual species to those of the entire assemblage.

SAMPLING BIAS

Our index of feeding preference may have overestimated importance of small-seeded fruits. Passage of seeds from such fruits is spread over a longer period than seeds from few- or one-seeded fruits (Levey 1986, 1987b). Nonetheless, within a fruit species or group of small-seeded fruits, seasonal and annual comparisons of this index are valid. Moreover, small-seeded species were not favored by all birds, indicating that potential biases from differences in seed passage time did not affect qualitative interpretations.

Birds that mandibulate fruits ("mashers") often drop seeds (Moermond and Denslow 1985, Levey 1987b). Consequently, large-seeded fruits may be underestimated; we have, however, recorded a wide array of seeds, varying in length from 0.3 mm to about 12 mm, in their diets.

RESULTS

DIET BREADTH

We recorded 226 fruit species in samples from 80 bird species at all five sites combined. Frugivores were most abundant and diverse in the young second-growth site, even after accounting for differences in sample effort (Table 1; Blake et al., in press). By contrast, average number of

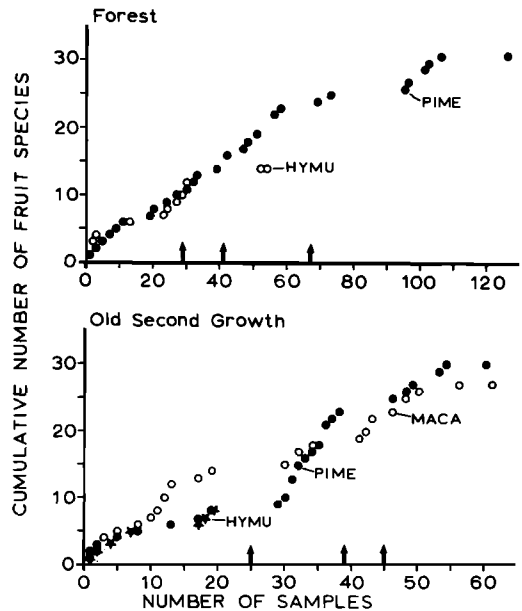


FIGURE 1. Fruit species accumulation curves for representative birds from old second-growth and forest habitats in Costa Rica. PIME = Red-capped Manakin, HYMU = Wood Thrush, and MACA = White-collared Manakin. Arrows along the ordinate axis point to data from a new season for MACA in old second-growth and PIME in forest.

fruit species in diets of birds overall (total number of fruit species/total number of bird species; Table 1) was lower there than at older sites. Average diversity of fruits in diets was greatest for birds of forest at 1000 m. General trends found in number of frugivores and average dietary diversity among sites were paralleled by trends in abundance and diversity of fruiting plants at each site. Fruit abundance was significantly higher during all seasons in the youngest site than in either of the older lowland sites (Loiselle 1987, see also Levey 1988). Total species richness of fruiting plants, however, was greater in old second-growth and primary forest sites than in the youngest site (Loiselle 1987).

Fruit species still were being added to diets of birds even after 100 fecal samples had been examined (Fig. 1). All three models used to fit accumulation curves produced highly significant ($P < 0.001$) results. The exponential (semi-log) function provided the best fit in only a few cases and few species reached an asymptote with respect to diet diversity. Linear and power functions provided the best fit in an equal number

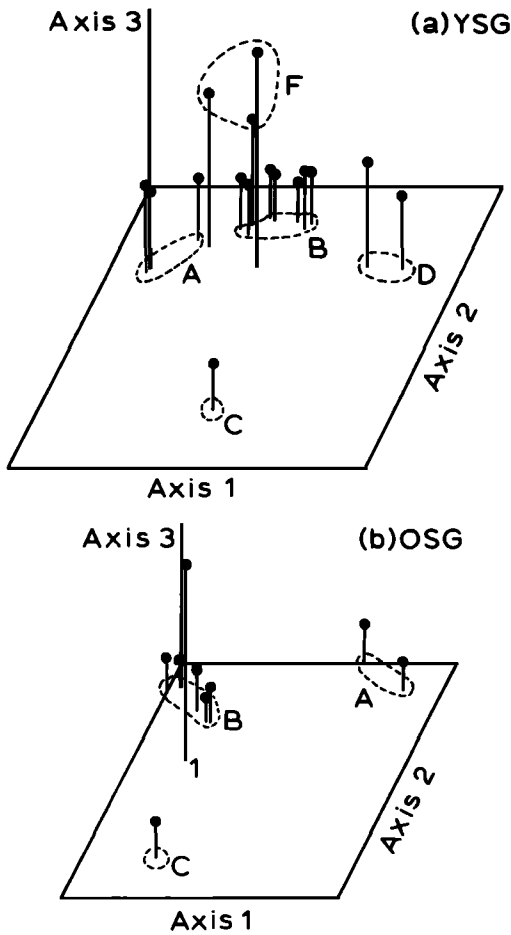


FIGURE 2. Ordination of fruit-eating birds in fruit-species space from (a) young second-growth (YSG) and (b) old second-growth (OSG). Birds are plotted according to their factor scores along first three ordination axes (see Table 2). For young second-growth, Group A = Orange-billed and Black-striped sparrows, and Red-throated Ant-Tanager; Group B = Grey-cheeked, Swainson's, and Wood thrushes, Red-capped and White-collared manakins, Grey-capped Flycatcher, and Grey Catbird; Group C = Ochre-bellied Flycatcher; Group D = Clay-colored and Pale-vented robins; Group F = Scarlet-rumped and Crimson-collared tanagers, and Buff-throated Saltator. For old second-growth, Group A = Red-throated Ant-Tanager and Orange-billed Sparrow; Group B = Dusky-faced Tanager, White-collared and Red-capped manakins, and Swainson's and Wood thrushes; Group C = Ochre-bellied Flycatcher. "1" refers to White-ruffed Manakin (OSG), a bird not readily classified into any group.

of cases. An apparently continuous increase in diet breadth was due partially to differences in plant phenologies; new species were added to the diet as they became available seasonally (Fig. 1).

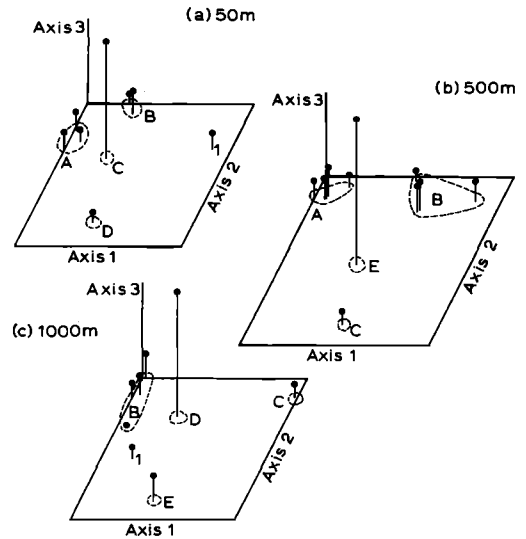


FIGURE 3. Ordination of fruit-eating birds in fruit species space from forest at (a) La Selva, 50-m, (b) 500-m, and (c) 1000-m. Birds are plotted according to their factor scores along the first three ordination axes (see Table 3). For 50-m, Group A = Olive and Tawny-crested tanagers, and White-ruffed Manakin; Group B = Red-capped Manakin and Wood Thrush; Group C = Ochre-bellied Flycatcher; Group D = Pale-vented Robin. For 500-m, Group A = Orange-billed Sparrow, White-ruffed Manakin, and Tawny-crested and Olive tanagers; Group B = Red-capped Manakin, Black-faced Solitaire, and *Catharus* and Wood thrushes; Group C = Ochre-bellied Flycatcher; Group E = Tawny-capped Euphonia. For 1000-m, Group B = Slaty-backed Nightingale-Thrush, Swainson's Thrush, White-crowned Manakin, and Black-faced Solitaire; Group C = Olive-striped Flycatcher; Group D = Pale-vented Robin; Group E = Tawny-capped Euphonia. "1" refers to Swainson's Thrush (50-m) or Common Bush-Tanager (1000-m), birds not readily classified into any group.

Despite the continued addition of fruit species with increased sample effort, consistency of guild composition among sites (discussed below) suggests that our sample sizes were adequate to describe the frugivorous bird assemblages through ordination techniques.

If frugivores feed opportunistically, diet diversity should increase more rapidly (i.e., have a higher slope) in habitats that support a wider diversity of fruits (e.g., primary forest understory vs. young second-growth). To test that prediction, we compared slopes of fruit species accumulation curves for four frugivore species that were common in two or three lowland sites (Orange-billed Sparrow, Ochre-bellied Flycatcher,

TABLE 2. CORRELATION (PEARSON'S r) OF FRUIT VARIABLES WITH MAJOR AXES GENERATED BY BRAY-CURTIS ORDINATION OF THE FRUIT-EATING BIRD ASSEMBLAGE IN SECOND-GROWTH HABITATS IN COSTA RICA (SEE TEXT). ONLY VARIABLES WITH SIGNIFICANT CORRELATIONS ($P < 0.05$) ARE SHOWN. DESCRIPTION OF FRUIT VARIABLES IN APPENDIX 2

Young second-growth				Old second-growth			
Variable	Axis 1	Axis 2	Axis 3	Variable	Axis 1	Axis 2	Axis 3
ARILAT		0.900		ARIL		0.961	
ATTARIL		0.905		LGSDUN			0.940
TERMUN		-0.673		HENOSS			0.740
AXIL	-0.802			CLIBES			
AGGREG			0.944	WITAST			
FICUS	0.708			TERMUN			
TREE1	0.857			FICUS	0.847		0.838
TREES			0.673		0.796		
PASSIF			0.554		-0.838		

Red-capped Manakin, and White-collared Manakin) using equal sample sizes for slope comparisons. Only data for Orange-billed Sparrows supported the hypothesis: fruits were added in the diet at a more rapid rate (higher slope) in older than in younger second-growth ($t = 4.2$, $P < 0.001$). Ochre-bellied Flycatchers actually accumulated fruit species faster in young habitats ($t = 3.6$, $P < 0.001$).

ORDINATION OF FRUIT-EATING BIRD ASSEMBLAGES

Primary factors separating bird species by diet varied among sites (Tables 2, 3), but a series of distinct groups could be identified (Figs. 2, 3). Interpretation of different groups was based on correlations of fruit variables with major ordination axes for each site. Not all groups were represented at each site and some species fit into different groups at different sites.

Two groups (A and B) were composed of species that fed on different sets of understory fruits. Group A included species that fed on small-seeded axillary or cauliflorous fruits. Group B species preferred understory plants with berries displayed on terminal infructescences or with relatively large seeds. Group B was represented by 2 to 7 species at each site, whereas Group A included 2 to 3 species. Group A was not represented among birds at the highest (1000-m) site (Fig. 3c).

Two groups (C and E) were each represented by a single species. Group C species fed principally on arillate fruits and were present at all sites. The Tawny-capped Euphonia fed heavily on fruits of the epiphytic genus *Anthurium* and formed a separate guild (E) at 500 m and 1000 m (Figs. 3b, c). Unlike its lowland counterparts,

this euphonia characteristically fed in the understory, most likely because *Anthurium* is more abundant in the understory of highland forests than in lowland forest (Loiselle 1987).

Guild D was composed of birds that fed primarily at subcanopy or canopy levels. It was represented by a single species in lowland and 1000-m forest and was not among common fruit-eating birds captured in the understory of forest at 500 m or in old second-growth.

A final frugivore guild (F) was present only in young second-growth and consisted of two tanagers and a saltator (Fig. 2a). These three species ate a variety of fruits, including *Piper* fruits, whereas most other species only fed rarely on *Piper* or not at all. Since those three species mandibulate fruits, as do members of Group A, their separation into a distinct subset of frugivores, as well as the close alignment along the major axis with fruit-eaters that swallow fruits whole, argues that seed passage rates did not overtly bias the data.

Some species, most notably Swainson's Thrush, did not fit well or consistently into any guild. Swainson's Thrushes primarily are passage migrants through Costa Rica, rarely wintering at La Selva. Their diet thus was restricted to those fruits available during the short time they were present. Similarly, White-ruffed Manakins are altitudinal migrants that descend for two to four months each year to lowland sites at La Selva, where they prefer primary forest. They were present for only a short time in our old second-growth site during January and February 1986 and fed almost exclusively on two species of fruits.

Our sample sizes for most *Tangara* species in forest at 1000 m were too small ($N < 5$) to warrant inclusion into an ordination now. We believe that, once included, they will form a new

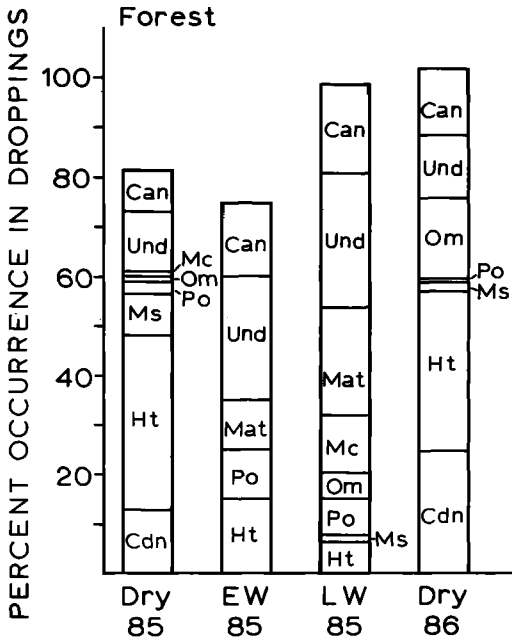


FIGURE 7. Percent occurrence of common fruiting plants in the diets of birds in lowland forest and over four seasons. Percent occurrence may exceed 100% because fecal samples often contained more than one seed type. Abbreviations are in Figures 4, 5, and 6.

noted. Fruit preferences varied more among species in young and old second-growth, as might be expected if fruits were competing for birds at those sites. Red-capped Manakins, for example, avoided *Clidemia dentata*, whereas other species showed weak to strong preferences for it. Scarlet-rumped Tanagers, unlike most other species, preferred *Piper* and *Passiflora* fruits.

SEASONAL AND ANNUAL VARIATION IN FRUIT USE

We analysed seasonal and annual variation in use of fruits produced by seven common fruiting plants at each lowland site. Those plants accounted for 79 to 84% of the total ripe fruit available in the understory (known bird-dispersed plants only) at those sites (Fig. 4).

Seasonal variation

Continuously-fruiting species were more common in the youngest site than in the other two lowland sites, and fruit use by birds was influenced by those phenological patterns. Thus, preference or avoidance of common fruits in young second-growth reflected choice of fruits rather than changes in plant phenologies. *Conostegia*

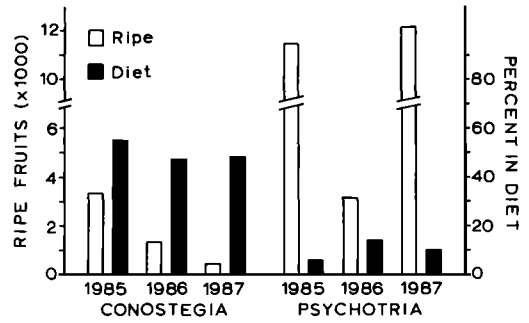


FIGURE 8. Number of ripe fruits of *Conostegia subcrustulata* (Cs) and *Psychotria pittieri* (Pp) and their percent occurrence in the diets of birds over three dry seasons in young second-growth. The number of ripe fruits available are directly comparable among years because the same quadrats and area were sampled in all three years. Note that the peak occurrence of ripe *P. pittieri* fruits was approximately two months earlier in 1986 (see Fig. 4).

subcrustulata fruited year round at the youngest site (Fig. 4) and was represented in over 40% of fecal samples during all seasons (Fig. 5). In fact, all common fruiting plants, with the exception of *Miconia affinis* in late wet season 1985, appeared in diets of birds during each season in young second-growth. *Miconia affinis*, a fruit relatively rich in sugar content (15.8%, Moermond and Denslow 1983), was unusual in its highly aseasonal production of fruits in young second-growth. When it was available, birds preferred *Miconia* and ate fewer other, generally favored fruits.

Only four species occurred in diets of birds in old second-growth during each season (Fig. 6). *Miconia affinis* was recorded as present in diets of some species, even though we did not record ripe fruits during all seasons (Fig. 4). We often observed birds feeding on unripe or partially ripe berries of that fruit. At the forest site, *Henrietella tuberculosa* and *Psychotria officinalis* occurred in diets of birds during all seasons (Fig. 7), even though our samples failed to detect fruiting of the former species year-round.

Considerable seasonal variation in fruit use occurred at all sites (Table 6), particularly among understory fruits. Use of canopy fruits did not vary in older forests (Table 6), suggesting that birds did not move up into canopy habitats at any one time of the year (see also Loiselle 1988).

Annual variation (dry season samples)

Annual variation in fruit use was pronounced at the young second-growth site (Table 6), but

TABLE 4. INDEX OF FRUIT USE (D_{fr}) BY BIRDS FOR COMMON FRUITING PLANTS AT THREE COSTA RICAN LOWLAND SITES. D_{fr} WAS CALCULATED BY SUMMING DATA FROM ALL SEASONS IN WHICH RIPE FRUIT WAS AVAILABLE. SIGNIFICANCE OF INDICES WAS TESTED BY COMPARING OCCURRENCE OF THE FRUIT IN THE BIRDS' DIETS TO THAT EXPECTED FROM THE AVAILABILITY OF RIPE FRUIT

Fruit species	D_{fr}	P	Fruit species	D_{fr}	P
Young second-growth			Lowland forest		
<i>Conostegia subcrustulata</i>	0.78	***	<i>Clidemia densiflora</i>	-0.24	**
<i>Miconia affinis</i>	0.57	***	<i>Henrietella tuberculosa</i>	0.17	ns
<i>Clidemia dentata</i>	0.66	***	<i>Ossaea macrophylla</i>	-0.46	***
<i>Psychotria brachiata</i>	-0.56	**	<i>Miconia simplex</i>	0.24	ns
<i>Psychotria pittieri</i>	-0.86	***	<i>Psychotria officinalis</i>	-0.84	***
<i>Passiflora auriculata</i>	0.50	***	<i>Miconia centrodesma</i>	-0.25	ns
<i>Piper sancti-felices</i>	0.52	***	<i>Miconia "attenuate"</i>	-0.07	ns
Old second-growth					
<i>Clidemia dentata</i>	0.28	*			
<i>Miconia affinis</i>	-0.42	***			
<i>Siparuna</i> sp.	0.53	***			
<i>Witheringia asterotricha</i>	-0.48	***			
<i>Leandra</i> sp.	-0.22	ns			
<i>Psychotria grandis</i>	-0.78	***			
<i>Psychotria racemosa</i>	0.32	ns			

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ns = not significant.

less pronounced in older sites. Because sample sizes from the young second-growth site were larger, a statistically significant χ^2 value was easier to obtain and annual variation in fruit use at that site may be overestimated relative to older lowland sites. Higher annual variation at that site also may have been due to the inclusion of 1987 data, but this is unlikely for two reasons. First, analysis of capture data revealed that 1985 and 1987 were more similar to each other at all sites than to capture data during 1986 (Blake et al. in press). Second, we have observed greater changes in the structure of vegetation through plant mortality and growth at the young site than in either old second-growth or forest sites.

A further illustration of annual variation at the young second-growth site is provided by comparing occurrence of two common fruits, *Conostegia subcrustulata* and *Psychotria pittieri*, in diets (Fig. 8). Abundance of ripe *Conostegia* fruits during the dry season declined steadily from 1985 to 1987, although the proportional representation of this fruit in diets of birds did not change among years ($\chi^2 = 3.7$, $df = 2$, $P > 0.10$). In contrast, use of *Psychotria pittieri*, an alternative, less preferred fruit (Table 4), increased from 1985 ($\chi^2 = 9.8$, $df = 2$, $P < 0.01$).

DISCUSSION

FRUGIVORE GUILDS

Previous studies on understory tropical bird communities often recognized a variety of in-

sectivore guilds (e.g., foliage-gleaning, bark, and terrestrial), but only one frugivore guild (e.g., Terborgh and Robinson 1986). Our results show, however, that tropical understory frugivores partition fruit resources. The nonrandomness of the different frugivore guilds was revealed by the consistency of guild composition among sites.

Frugivore guilds, which represented birds that made similar foraging decisions in the field, were separated largely because of differences in morphology and foraging methods. For example, in young second-growth, the Red-throated Ant-Tanager, and Black-striped and Orange-billed sparrows foraged low in the undergrowth or on the ground and rarely ascended into taller shrubs or treelets. All three species have relatively longer tarsi than other emberizids (Loiselle and Blake, unpubl. data) and thus have greater difficulty reaching for fruit from a perch (Moermond and Denslow 1985). Consequently, they characteristically fed on axillary (easily accessible) fruits from low shrubs; terminal (less accessible) fruits were less preferred. In contrast, *Ramphocelus* tanagers and Buff-throated Saltators, with relatively shorter tarsi and, thus, greater perching and reaching ability (Moermond and Denslow 1985), foraged at all heights in young second-growth and fed on a wider range and diversity of fruits than the ant-tanager and sparrows.

Two guilds (C, E) represented birds that specialized on epiphytic (e.g., *Anthurium* sp.) or arillate fruits (e.g., *Clusia* sp.) and consequently, those guilds were defined largely by fruit type.

TABLE 5. INDEX OF FRUIT USE (D_{it}) FOR COMMON FRUITING PLANTS BY THREE OR FOUR COMMON FRUIT-EATING BIRDS IN EACH OF THREE COSTA RICAN LOWLAND SITES

Fruit species	Red-capped Manakin	White-collared Manakin	Scarlet-rumped Tanager	Orange-billed Sparrow	Dusky-faced Tanager	Olive Tanager	Wood Thrush
Young second-growth							
<i>Conostegia subcrustulata</i>	0.74	0.78	0.95	0.23			
<i>Miconia affinis</i>	0.44	0.62	0.36	0.00			
<i>Clidemia dentata</i>	-1.00	0.20	0.90	0.93			
<i>Psychotria brachiata</i>	-1.00	0.32	-0.49	-1.00			
<i>Psychotria pittieri</i>	-0.97	-0.78	-0.90	-0.93			
<i>Passiflora auriculata</i>	-1.00	0.00	0.88	-1.00			
<i>Piper sancti-felicitis</i>	0.11	-0.42	0.92	-1.00			
Old second-growth							
<i>Clidemia dentata</i>	-1.00	0.41		0.90	0.99		
<i>Miconia affinis</i>	-0.43	-0.22		-1.00	-1.00		
<i>Siparuna</i> sp.	0.23	0.53		-1.00	-1.00		
<i>Witheringia asterotricha</i>	-0.70	0.06		0.62	0.27		
<i>Leandra</i> sp.	0.42	0.23		0.56	0.56		
<i>Psychotria grandis</i>	-0.80	-0.89		-1.00	-1.00		
<i>Psychotria racemosa</i>	0.62	-1.00		-1.00	-1.00		
Lowland forest							
<i>Clidemia densiflora</i>	-0.37					0.46	0.28
<i>Henrietella tuberculosa</i>	0.27					0.72	0.33
<i>Ossaea macrophylla</i>	-0.48					-0.18	-0.68
<i>Miconia simplex</i>	0.61					0.71	0.84
<i>Psychotria officinalis</i>	-0.59					-1.00	-0.48
<i>Miconia centrodesma</i>	-0.05					-1.00	0.10
<i>Miconia "attenuate"</i>	0.50					-1.00	0.50

Most other fruit-eating birds in our analyses often took fruit on the wing by hovering or snatching (see Moermond and Denslow 1985), then swallowed the fruits whole. But several subgroups were identified based largely on foraging height. Feeding decisions, and thus guild composition, were constrained by morphology and influenced by feeding method, fruit type and display, and foraging height.

Does competition explain resource partitioning among frugivores in Costa Rica? This would require that fruit resources be limiting. Fruits may be in short supply in undisturbed forest understory (Foster 1982b), as several lines of evidence suggest. First, few fruits were observed to rot on forest understory plants, suggesting that ripe fruits were taken relatively rapidly. Second, birds have been observed feeding on unripe fruits when fruits were scarce (pers. obs.; also Foster 1977). Third, abundance of frugivores was correlated with abundance of ripe fruits (Blake and Loiselle, unpubl. data; Loiselle 1987; Levey 1988). Fourth, interspecific and intraspecific aggression at and defense of fruit resources has been observed (e.g., Lederer 1977, Martin 1982, Willson 1986).

Ripe fruit was often four-fold more abundant in young second-growth during our study than in forest understory (Loiselle 1987) and may not have been limiting during our study. We often observed fruits rotting on plants and found no correlation between frugivore abundance and ripe fruits. In young second-growth, it appears that fruits may compete for dispersers, rather than the reverse.

Alternatively, partitioning of fruit resources among frugivores may not reflect competition for fruits, but rather may reflect adaptations to exploit other resources, such as insects. Snow and Snow (1971) argued that tanagers and honeycreepers in Trinidad, which overlapped broadly in fruits consumed, coexisted because of their partitioning of insect resources (also Lack 1976a for Jamaican frugivores; but see Moermond and Denslow 1985). Predation also may influence fruit choice and foraging patterns of birds (Howe 1979, Martin 1985b, Snow and Snow 1986). We are not able to evaluate adequately the possible role of competition in structuring frugivore guilds in Costa Rica, but we agree with Fleming (1979) and Willson (1986) that it likely operates in resource partitioning. Particular attention in future

TABLE 6. SIGNIFICANCE VALUES FOR χ^2 ANALYSES TESTING THE OCCURRENCE OF FRUITS IN DIETS OF BIRDS RELATIVE TO OCCURRENCE OF ALL OTHER FRUIT SPECIES AT THREE COSTA RICAN LOWLAND SITES. "CANOPY" INCLUDED FRUITS OF ALL KNOWN CANOPY AND SUBCANOPY SPECIES RECORDED IN BIRDS' DIETS. OTHER "UNDERSTORY" INCLUDED ALL UNDERSTORY SPECIES IN BIRDS DIETS EXCEPT THOSE TESTED SEPARATELY

Fruit species	Seasonal variation in fruit use			Annual variation in fruit use		
	χ^2	df	P ^a	χ^2	df	P
Young second-growth						
<i>Conostegia subcrustulata</i>	35.5	4	***	3.7	2	0.15
<i>Miconia affinis</i>	379.2	3	***	19.4	2	**
<i>Clidemia dentata</i>	53.5	4	***	12.6	2	**
<i>Psychotria brachiata</i>	6.4	4	0.17	3.2	2	0.21
<i>Psychotria pittieri</i>	29.9	4	***	9.8	2	**
<i>Passiflora auriculata</i>				11.3	2	**
<i>Piper sancti-felicis</i>	9.5	3	*	3.3	2	0.20
Old second-growth						
<i>Clidemia dentata</i>	10.8	3	*	1.0	1	0.75
<i>Miconia affinis</i>	26.3	3	***	2.8	1	0.09
<i>Siparuna</i> sp.	10.1	3	*	2.2	1	0.14
<i>Witheringia asterotricha</i>	3.6	3	0.31	3.0	1	0.08
<i>Leandra</i> sp.				4.5	1	*
"Canopy"	3.9	3	0.27	1.8	1	0.18
Other "Understory"	10.6	3	*	0.8	1	0.38
Lowland forest						
<i>Clidemia densiflora</i>				4.8	1	*
<i>Henriettella tuberculosa</i>	24.4	3	***	0.2	1	0.68
<i>Ossaea macrophylla</i>	6.1	1	*			
<i>Miconia simplex</i>	9.4	2	**	7.0	1	**
<i>Psychotria officinalis</i>	13.2	3	**	1.7	1	0.19
<i>Miconia centrodesma</i>	7.6	1	**			
<i>Miconia "attenuate"</i>	1.4	1	0.23			
"Canopy"	3.4	3	0.33	1.6	1	0.20
Other "Understory"	10.8	3	*	0.1	1	0.85

^a * P < 0.05, ** P < 0.01, *** P < 0.001.

studies should be given to evaluating alternative hypotheses such as predation, mutualism, and abiotic interactions (Wiens 1977, Brown and Bowers 1984, Martin 1988c).

In contrast to tropical systems, many fewer

frugivore guilds, usually two, have been described in temperate forests. In Illinois, frugivore guilds were determined largely by foraging height, but because of annual variation and inconsistency in fruit preference by birds, no single factor explained foraging preference by birds (Katusic-Malmborg and Willson 1988). Sorenson (1981) also was unable to determine reasons for differences in fruit choice among British tits and thrushes.

SEASONAL AND ANNUAL VARIATION IN FRUIT USE

Even in the relatively aseasonal climate of Atlantic slope Costa Rica, fruit abundance varied seasonally (Frankie et al., 1974, Loiselle 1987) among lowland sites. In well lighted areas, more plants produced fruit continuously, whereas in shaded areas, production was highly seasonal (Fig. 4). Consequently, seasonal variation in fruit use by birds was influenced by different factors. In young second-growth, where fruits were more abundant and more species fruited year round, birds were more selective (see Schoener 1971b, Krebs et al. 1977). In contrast, although feeding preferences were observed in lowland forest, seasonal changes in fruit phenology there largely accounted for seasonal variation in fruit use.

The nature of seasonal variation in diet also varied among bird species. Most resident frugivores ate fruit year round and changes in feeding preference or fruit availability accounted for seasonal variation. Some winter residents, such as the Wood Thrush, ate fruit in substantial quantities only during late wet and late dry seasons, times when they were accumulating fat reserves for migration. Wheelwright (1988) demonstrated that even when fruit availability was held constant year round, American Robins showed seasonal variation in fruit use, indicating that physiological needs, and not fruit availability, influenced that seasonal variation.

In spite of large annual variation in fruit abundance and availability, birds of old second-growth and forest showed little annual variation in fruit use. Fruit abundance changed, but phenological patterns (what fruits were available) did not. In contrast, birds of young second-growth showed considerable annual variation, which we attribute to successional changes in vegetation at that site. Our data span only two or three years and interpretation of annual patterns is tentative at best.

FECAL SAMPLES AS A TOOL FOR ANALYSIS OF DIETS

Collection of fecal samples or regurgitated seeds to analyse diets is not new, but only Wheelwright

et al. (1984) used it to describe an assemblage of fruit-eating birds. They used a variety of techniques (fecal samples, behavioral observations of birds at fruiting trees, seed traps) and concluded that fecal samples and seed traps placed under display or nest perches generally were the most effective means of obtaining representative diet samples. Clearly, a combination of observational and fecal collection techniques is needed to describe diets in detail, but the difficulty of observing birds in the dark understory of tropical forests often may necessitate use of fecal samples there. Moreover, this method is quick, is not biased by observations at conspicuous plants bearing large fruit crops, and, we suspect, is more likely to include most fruits eaten by birds.

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APPENDIX I. ENGLISH AND SCIENTIFIC NAMES OF ALL BIRD SPECIES MENTIONED IN THE TEXT

Wedge-billed Woodcreeper (*Glyphorynchus spirurus*), Olive-striped Flycatcher (*Mionectes olivaceus*), Ochre-bellied Flycatcher (*Mionectes oleagineus*), Grey-capped Flycatcher (*Myiozetetes granadensis*), White-collared Manakin (*Manacus candei*), White-ruffed Manakin (*Corapipo leucorrhoa*), White-crowned Manakin (*Pipra pipra*), Red-capped Manakin (*Pipra mentalis*), Black-faced Solitaire (*Myadestes melanops*), Slaty-backed Nightingale-Thrush (*Catharus fuscater*), Grey-checked Thrush (*Catharus minimus*), Swainson's Thrush (*Catharus ustulatus*), Wood Thrush (*Hylocichla mustelina*), Pale-vented Robin (*Turdus obsoletus*), Clay-colored Robin (*Turdus grayi*), American Robin (*Turdus migratorius*), Grey Catbird (*Dumetella carolinensis*), Tawny-capped Euphonia (*Euphonia anneeae*), Olive Tanager (*Chlorothraupis carmioli*), Tawny-crested Tanager (*Tachyphonus delatrii*), Red-throated Ant-Tanager (*Habia fuscicauda*), Crimson-collared Tanager (*Ramphocelus sanguinolenta*), Scarlet-rumped Tanager (*Ramphocelus passerinii*), Common Bush-Tanager (*Chlorospingus ophthalmicus*), Dusky-faced Tanager (*Mitrospingus cassinii*), Buff-throated Saltator (*Saltator maximus*), Orange-billed Sparrow (*Arremon aurantiirostris*), Black-striped Sparrow (*Arremonops conirostris*)

APPENDIX II. DESCRIPTION OF FRUIT VARIABLES USED IN ORDINATION OF COSTA RICAN FRUIT-EATING BIRD ASSEMBLAGES (SEE TABLES 2, 3). SEE TEXT FOR DESCRIPTION ON HOW FRUIT VARIABLES WERE DEFINED. SITES AT WHICH FRUIT VARIABLES WERE USED ARE IDENTIFIED. Y = YOUNG SECOND-GROWTH, O = OLD SECOND-GROWTH, L = LOWLAND FOREST AT LA SELVA, M = FOREST AT 500-M, H = FOREST AT 1000-M

Variable	Site	Description
AGGREG	Y	Includes aggregate fruits, e.g., <i>Cecropia</i> , <i>Piper</i>
ANTHUR	O, H	Fruits of <i>Anthurium</i>
ANTBRO	M	Fruits of aroids and bromeliads
ARILAT	Y	Arillate fruits with thin layer of pulp surrounding entire seed, seed usually large, e.g., <i>Alchornea</i> , <i>Dollicarpus</i> , <i>Dieffenbachia</i>
ATTARIL	Y	Aril attached to one end of seed only, e.g., <i>Siparuna</i> , <i>Calathea</i> , <i>Renealmia cernua</i>
ARIL	O, L, M, H	Includes both ARILAT and ATTARIL
AXIL	Y, L, M, H	Includes juicy berries presented in axils or along stems, e.g., <i>Clidemia</i> , <i>Besleria</i> , <i>Witheringia</i> , <i>Sabicea</i> , many seeded
BROMEL	H	Fruits of bromeliads
CLBASP	Y	Fruits of the Compositae: <i>Clibadium asperum</i> (Aubl.) DC.
CLIBES	O	A subset of AXIL group, includes juicy fruits of <i>Clidemia</i> , <i>Besleria</i> , and <i>Sabicea</i>
EPISHB	M, H	Fruits of epiphytic shrubs, e.g., <i>Cavendishia</i> , <i>Blakea</i> , <i>Topo-bea</i>
FIGUS	Y, O	Fruits of <i>Ficus</i>
HELIC	Y	Fruits of <i>Heliconia</i> species

APPENDIX II. CONTINUED

HENOSS	O, L, M	Fruits of some Melastomataceae, e.g., <i>Henriettella</i> and <i>Ossaea</i>
LGSDUN	all	Large seeded understory fruit from shrubs or small trees, e.g., <i>Ardisia</i> , <i>Neea</i> , <i>Cestrum</i>
MICCAN	O, L, M	Canopy and subcanopy trees of <i>Miconia</i>
OSSAEA	H	Fruits of <i>Ossaea</i> species
PASSIF	Y	Fruits of <i>Passiflora</i> species
PHYRIV	Y, M	Fruits of <i>Phytolacca rivinoides</i> Kunth & Bouche
STYROF	Y	Includes a selected group of <i>Psychotria</i> fruits with a styrofoam rather than juicy texture
TERMUN	O, L, M	Juicy berries of understory shrubs presented on terminal infructescences
TREE1	Y, L	Single or few-seeded subcanopy or canopy trees, e.g., Lauraceae, <i>Hampea</i>
TREES	Y, L	Many-seeded subcanopy or canopy trees, e.g., <i>Dendropanax</i> , <i>Hieronyma</i> , <i>Vismia</i>
TREE	O, M, H	Includes TREE1 and TREES
UNK112	H	An unidentified species in the diets of birds at 1000 m, relatively common in some birds
VINE	Y, O, H	Large-seeded vines, e.g., <i>Cissus</i> , <i>Cissampelos</i>
WITAST	O, L	A subset of the AXIL group, includes juicy fruits of Solanaceae