ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/251734673

Fruits in the Diets of Neotropical Migrant Birds in Costa Rica

Article *in* Biotropica · June 1992

DOI: 10.2307/2388674

CITATIONS
98

READS
211

2 authors:

John G Blake
University of Florida

Bette A Loiselle
University of Florida

139 PUBLICATIONS 5,485 CITATIONS

SEE PROFILE

125 PUBLICATIONS 14,074 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Project Mating success, foraging costs and behavior of manakins (Pipridae) in Brazil View project

Project Changes in land-cover and vegetation and their implications in Ecuador View project

All content following this page was uploaded by John G Blake on 19 October 2018.

The user has requested enhancement of the downloaded file.

BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Fruits in the Diets of Neotropical Migrant Birds in Costa Rica
Author(s): John G. Blake and Bette A. Loiselle
Source: *Biotropica*, Vol. 24, No. 2, Part A (Jun., 1992), pp. 200-210
Published by: The Association for Tropical Biology and Conservation
Stable URL: http://www.jstor.org/stable/2388674
Accessed: 16-09-2015 14:57 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

The Association for Tropical Biology and Conservation is collaborating with JSTOR to digitize, preserve and extend access to *Biotropica.*

http://www.jstor.org

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

BIOTROPICA 24(2a): 200–210 1992

Fruits in the Diets of Neotropical Migrant Birds in Costa Rica[1]

John G. Blake and **Bette A. Loiselle**

Department of Biology, University of Missouri–St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121, U.S.A.

ABSTRACT

We used fecal samples collected from birds captured in mist nets to determine the occurrence of fruit in the diets of neotropical migrant birds (species that breed in North America and winter in Central and South America) at six study sites in Costa Rica. A total of 1016 migrants representing 30 species were captured. Fecal samples were collected from 85 percent of all birds captured. Fruits (seeds, pulp) occurred in 58 percent of all fecal samples; the proportion of fecal samples containing fruit ranged from 0 percent (9 species) to over 90 percent (9 species). Individual fecal samples contained seeds from as many as 4 species of plants. At least 98 plant species from at least 29 plant families were represented in fecal samples. Species of Melastomataceae accounted for 37 percent and those of Rubiaceae for 16 percent of all species recorded. Number of fruit species in diets of individual migrant species ranged from 0 (9 species) to 63 (Swainson's Thrush, *Catharus ustulatus*). Our data demonstrate that some migrants may rival permanent residents in the diversity of fruits they consume. A shift to increased frugivory in the late dry season, as birds were preparing to migrate north, was noted.

A MAJORITY OF BIRDS THAT BREED in temperate North America spend most of the year in the tropics ("neotropical migrants" hereafter; Rappole *et al.* 1983). Despite much recent attention given to apparent declines in breeding populations of many of these species (*e.g.,* Terborgh 1989, Askins *et al.* 1990, Hagan & Johnston, in press), the habitat requirements and diets of most species are poorly known during nonbreeding seasons (Keast & Morton 1980). Yet understanding habitat and diet requirements of neotropical migrants throughout the year is necessary if we are to understand population dynamics of these species and develop adequate plans for their conservation. Population declines of neotropical migrants are, for example, most likely a consequence of events on both breeding and wintering grounds (Hutto 1989, Terborgh 1989, Askins *et al.* 1990, Blake *et al.,* in press) (*e.g.,* breeding habitat fragmentation, tropical deforestation).

Most neotropical migrants feed primarily on insects during the breeding season; many, however, eat much fruit while in the tropics (Morton 1971, 1980; Leck 1972a, b; Howe & DeSteven 1979; Martin 1985b; Martin & Karr 1986; Blake *et al.* 1990; Loiselle & Blake 1990) and may be important seed dispersers for some plants (Greenberg 1981). Despite the apparent importance of fruit as a resource, little quantitative information on the occurrence of fruit in the diets of most overwintering migrants is available. Previous studies that have reported on diets of migrants in the tropics have tended to focus on relatively few species or on use of one specific plant species by different birds (*e.g.,* Morton 1971, Greenberg 1981). A comprehensive analysis of migrant diets from any location, similar to the analysis of all fruit-eating birds at Monteverde, Costa Rica, by Wheelwright *et al.* (1984), has not been presented previously.

We have been studying habitat use and diets of migrant (and nonmigrant) birds in several habitats in Costa Rica since 1985 (Loiselle 1987b, Blake *et al.* 1990, Blake & Loiselle 1991, Loiselle & Blake 1991). Elsewhere (Blake & Loiselle, in press) we report on patterns of habitat use by neotropical migrants. Here we summarize data collected on diets of migrants at our study sites.

STUDY AREA

Study sites were on the Caribbean slope of the Cordillera Central in northeast Costa Rica. Lowland habitats were 5–10 yr second-growth (one site), 25–35 yr second-growth (one site), and primary (undisturbed) forest (two sites) at the La Selva Biological Station (10°25′N, 84°01′W), a field station of the Organization for Tropical Studies. We also sampled diets of birds in primary forest at 500 m (one site at 10°20′N, 84°04′W) and at 1000 m (one site at 10°16′N, 84°05′W) in Braulio Carrillo National Park, about 15 and 20 km south of La Selva, respectively. Detailed descriptions of these study sites are in Blake and Loiselle (1991) and Loiselle and Blake (1991).

[1] Received 10 December 1990, revision accepted 15 July 1991.

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

La Selva receives about 3900 to 4000 mm rain annually (Hartshorn 1983, Organization for Tropical Studies, pers. comm.). 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 and 1000 m sites, but annual rainfall probably exceeds 4500 mm at both. General descriptions of La Selva and Braulio Carrillo are in Hartshorn (1983), Pringle *et al.* (1984), and Hartshorn & Peralta (1988).

METHODS

Mist nets (12-m, 4-shelf, 36-mm mesh) were used to sample birds in the lower levels of each habitat (Blake & Loiselle 1991, Loiselle and Blake 1991). Captured birds were banded, weighed, held for collection of fecal samples, and released at the point of capture. We collected samples every 5 to 6 weeks from January 1985 through April 1986 and from December to April 1986–1987 and 1987–1988.

Diet analyses were based on seeds and pulp from feces or regurgitated material (hereafter referred to collectively as "fecal samples") from mist netted birds. We placed captured birds in plastic containers lined with filter paper for 5 to 15 min. 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 genus because we could not distinguish species (*e.g., Anthurium, Ficus*). Further details are in Loiselle and Blake (1990).

The advantages and disadvantages of using fecal samples to determine diets of birds have been discussed elsewhere (Wheelwright *et al.* 1984, Loiselle & Blake 1990); here we summarize previous discussions. Differential passage rates of small and large seeds (Levey 1986, 1987) may lead to an overestimation of the importance of small-seeded fruits in diets of some bird species. Further, some birds may drop rather than ingest seeds of some fruits (Moermond & Denslow 1985, pers. comm.), leading to an underestimation of those fruits in the diet. Similarly, seeds of some fruits are regurgitated rather than defecated by some bird species; regurgitation often occurs, however, while the birds are being held. Despite these problems, collection of fecal samples is an effective way to gather data on fruit consumption (Wheelwright *et al.* 1984, Loiselle & Blake 1990). Fecal samples are not subject to many of the biases inherent in direct observations of fruit consumption. Birds foraging in forest understory frequently are hard to observe, so that visual records of fruit consumption often are incomplete or are biased by observations at conspicuous plants with large crops.

RESULTS

We captured 1016 migrants representing 30 species (Table 1). The most common species included Wood Thrush, Swainson's Thrush, Ovenbird, and Kentucky Warbler which together comprised 72 percent of all migrants captured. We collected 864 fecal samples. The number of fecal samples collected from different bird species ranged from 1 (6 species) to 259 (Wood Thrush) (Table 1). All 30 migrant species consumed insects, as indicated by presence of insect parts and uric acid in most (83%) fecal samples. Percentage of samples with insects ranged from 11 percent (Eastern Kingbird) to 100 percent (21 species).

Fruit seeds or pulp occurred in 58 percent of all fecal samples. The percentage of species-specific samples with fruit ranged from 0 (for 9 species) to over 90 (in 9 other species, including 4 represented by >5 fecal samples). All species represented by at least 5 samples consumed some fruit, except for Mourning Warbler and Canada Warbler (Table 1). Highly frugivorous species included Swainson's Thrush, Gray-cheeked Thrush, Eastern Kingbird, Gray Catbird, and Traill's Flycatcher. More than one fruit species often occurred in a single fecal sample (Table 1); Gray-cheeked Thrushes averaged two fruit species per sample, for example. The maximum number of fruit species represented in a single dropping was four.

We recorded at least 98 plant species from at least 29 families (Appendix) in samples collected from 21 of the 30 species of neotropical migrants captured (Table 2). (The actual number of species represented is probably higher because seeds of some samples were identified only to genus.) Most plant species were either members of the Melastomataceae (35 species) or Rubiaceae (16 species), two of the most common families in the understory of our study sites at La Selva and Braulio Carrillo (Loiselle 1987a).

Number of identified fruit species in diets of bird species ranged from 1 (4 bird species) to 52 (Wood Thrush) and 63 (Swainson's Thrush). Over half (58) of all fruit species were recorded in the diets of only one bird species; 27 plant species occurred only in samples collected from Swainson's Thrushes and 22 species only from Wood Thrushes. Plant species consumed by the greatest number of

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

TABLE 1. *Number of captures and number of fecal samples collected from migrants. Number and percent (in parentheses) of samples with insect parts or with fruit seeds or pulp are indicated. Mean, SD, and maximum number of plant species represented in a fecal sample are given for samples with fruits.*

Bird species	Bird code	Total captures	Total fecal samples	Samples with		Plant species		
				Insects	Fruits	Mean	SD	Max
Yellow-bellied Flycatcher *Empidonax flaviventris*	EMFL	4	1	1 (100)	0 (0)			
Acadian Flycatcher *E. virescens*	EMVI	40	23	23 (100)	6 (26)	1.0	0.0	1
"Traill's" Flycatcher *Empidonax* sp.[a]	EMTR	24	20	17 (85)	14 (70)	1.0	0.0	1
Great Crested Flycatcher *Myiarchus crinitus*	MYCR	10	10	10 (100)	6 (60)	1.17	0.41	2
Eastern Kingbird *Tyrannus tyrannus*	TYTY	9	9	1 (11)	9 (100	1.56	0.88	3
Veery *Catharus fuscescens*	CFUS	1	1	1 (100)	1 (100)	2		
Gray-cheeked Thrush *C. minimus*	CAMI	24	23	20 (87)	22 (96)	2.0	0.98	4
Swainson's Thrush *C. ustulatus*	CAUS	206	199	105 (53)	196 (98)	1.41	0.70	4
Wood Thrush *Hylocichla mustelina*	HYMU	303	259	240 (93)	154 (59)	1.29	0.62	4
Gray Catbird *Dumetella carolinensis*	DUCA	47	43	27 (63)	41 (95)	1.34	0.53	3
Red-eyed Vireo *Vireo olivaceus*	VIOL	2	2	1 (50)	2 (100)	1.0	0.0	1
Blue-winged Warbler *Vermivora pinus*	VEPI	3	3	3 (100)	1 (33)	1		
Golden-cheeked Warbler *V. chrysoptera*	VECH	4	4	4 (100)	0 (0)			
Chestnut-sided Warbler *Dendroica pensylvanica*	DEPE	45	44	44 (100)	8 (18)	1.0	0.0	1
Magnolia Warbler *D. magnolia*	DEMA	1	1	1 (100)	0 (0)			
Blackburnian Warbler *D. fuscus*	DFUS	2	2	2 (100)	1 (50)	1		
Bay-breasted Warbler *D. castanea*	DECA	3	3	3 (100)	2 (67)	1.0	0.0	1
Black-and-white Warbler *Mniotilta varia*	MNVA	3	3	3 (100)	0 (0)			
Worm-eating Warbler *Helmitheros vermivorus*	HEVE	19	14	14 (100)	3 (21)	1.0	0.0	1
Ovenbird *Seiurus aurocapillus*	SEAU	113	81	81 (100)	18 (22)	1.17	0.38	2
Northern Waterthrush *S. noveboracensis*	SENO	6	2	2 (100)	0 (0)			
Louisiana Waterthrush *S. motacilla*	SEMO	5	4	4 (100)	0 (0)			
Kentucky Warbler *Oporornis formosus*	OPFO	109	86	86 (100)	10 (12)	1.0	0.0	1
Mourning Warbler *O. philadelphia*	OPPH	11	9	9 (100)	0 (0)			
Hooded Warbler *Wilsonia citrina*	WICI	4	1	1 (100)	0 (0)			
Canada Warbler *W. canadensis*	I	6	6	6 (100)	0 (0)			
Summer Tanager *Piranga rubra*	PIRU	8	7	6 (86)	4 (57)	1.25	0.50	2
Scarlet Tanager *Piranga olivacea*	PIOL	2	2	2 (100)	2 (100)	1.5	0.71	2

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

TABLE 1. *Continued.*

Bird species	Bird code	Total captures	Total fecal samples	Samples with Insects	Samples with Fruits	Plant species Mean	Plant species SD	Plant species Max
Rose-breasted Grosbeak *Pheucticus ludovicianus*	PHLU	1	1	1 (100)	1 (100)	1		
Northern Oriole *Icterus galbula*	ICGA	1	1	1 (100)	1 (100)	1		

[a] Mostly *Empidonax traillii.*

bird species included *Conostegia subcrustulata* (eaten by 16 species), *Miconia affinis* (13 species), and *Clidemia dentata* (10 species). All three species are in the Melastomataceae and produce small, juicy berries.

Overall, a higher proportion of samples from forest habitats contained fruit (Table 3), probably because many more generally nonfrugivorous species (*e.g.,* Ovenbird, Kentucky Warbler) were captured in second-growth habitats (see Blake & Loiselle, in press). Within individual migrant species, several (Table 3) were more frugivorous in the young second-growth site, where fruit was more abundant (see also Blake & Loiselle 1991).

Seasonal variation in frugivory (based on number of fecal samples containing fruit) was apparent (Fig. 1). When data from all species and sites were pooled, an increase in frugivory from early to late dry season was apparent ($\chi^2 > 14$, $P < 0.001$, all years; chi-square based on number of samples with and without fruit). The increase in fruit use late in the dry season corresponded to the period when many highly frugivorous migrants, particularly Swainson's Thrush, pass through La Selva on their way north. Other migrants, including winter residents, also may increase consumption of fruit prior to migration. The Wood Thrush, a common winter resident at La Selva, showed a statistically significant increase in frugivory from early to late dry season during 1987 and 1988 (Fig. 1; 1985: $\chi^2 = 0.65$, $P > 0.50$; 1986: $\chi^2 = 3.4$, $P < 0.20$; 1987 and 1988: $\chi^2 > 16$, $P < 0.001$).

DISCUSSION

Many species of migrants are known to consume fruit while on their nonbreeding grounds (Rappole *et al.* 1983). Over 80 species of neotropical migrant birds occur at La Selva Biological Station and in Braulio Carrillo National Park (Blake *et al.* 1990, Blake & Loiselle, in press). Most neotropical migrants at La Selva depend primarily on insects for food but about 20 percent feed primarily or extensively on fruit (Blake *et al.* 1990). This compares to approximately 30 percent of the total avifauna at La Selva (363 total species, excluding accidentals) that rely primarily on fruit. Two-thirds of the 30 migrant species captured during this study ate some fruit and fruit was represented in over 50 percent of all fecal samples collected.

The importance of fruit in the diets of migrants varies widely among species and is influenced by a variety of factors, including morphology and for-

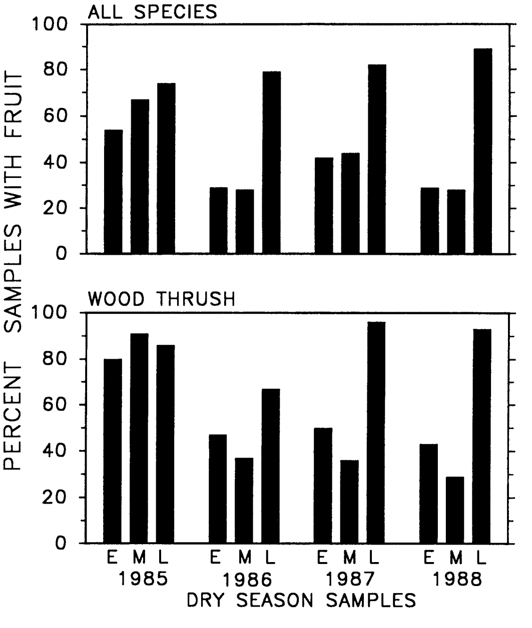

FIGURE 1. Percentage of fecal samples from all species and from Wood Thrush separately that contained fruit during early (E: late December–January), middle (M: February–mid March); and late (L: late March–April) dry seasons. Data are pooled from all habitats and study sites.

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

TABLE 2. *Number of fecal samples that contained fruit seeds or pulp. Bird species represented by <5 samples are listed at the end. Total birds = number of bird species (including those with <5 samples) that consumed the plant species; Total samples = number of fecal samples (all bird species) that contained seeds of that plant. Bird species codes are in Table 1; plant species codes are in Appendix.*

Plant ssp.	Bird species											Total birds	Total samples
	EMVI	EMTR	MYCR	TYTY	CAMI	CAUS	HYMU	DUCA	DEPE	SEAU	OPFO		
DENARB					2	10						2	12
SCHSYS						2	1					2	3
CECOBT							2					1	2
CLIASP						1		1				2	2
DOLDEN						3						1	3
PINCOR						4	5					3	10
BESCOL							3					1	3
NECMEM						12	3	2				3	17
HAMAPP							2	1				2	3
CLIDNS							19					1	19
CLIDEN		1	1		6	6	2	2	1	5	3	10	28
CONSUB	5	6	6	1	11	40	12	8	5	9	4	16	112
HENTUB							14					1	14
LEANDR							3					1	3
MICAFF		3		4		39	7	4	2	2	1	13	67
MICAPP						1	4					2	5
MICATT					1	3	3					3	7
MICBAR					3	1	1	1				4	6
MICBRE						2						1	2
MICCEN						4	3					2	7
MICMUL						5	4					2	9
MICNER						4	1					2	5
MICSIM						1	10					2	11
MICSMA						9	10					2	19
MIC110						3						1	3
MIC036						2						1	2
MIC280	1					1	2					3	4
OSSMAC							5					1	5
OSSSPP						2	1					2	3
CISSAM					1	3						2	4
FICCOL				2		9	1					3	10
AURAUR					1		2					2	3
AURNIG						7	5	3				3	15
PASAUR						2	1					3	4
PHYRIV						2	1	5				3	8

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

TABLE 2. *Continued.*

Plant ssp.	Bird species											Total birds	Total samples
	EMVI	EMTR	MYCR	TYTY	CAMI	CAUS	HYMU	DUCA	DEPE	SEAU	OPFO		
TRIPOL				1		2						2	3
BERGUI						2						1	2
CEPELA						3	4					2	7
HAMPAT					1	1						2	2
PSYBRA						3		1				2	4
PSYCOP						5	2					2	7
PSYGRA					1	2	1					3	4
PSYORC						1		1				2	2
PSYOFF					1	6	3					3	10
PSYPIT					3	1	10	13				4	27
PSYPSY					6							1	6
SABVIL					1	5	2					3	8
SAB060						3						1	3
CESRAC					1	3						2	4
WITAST					1	2	5					3	8
UREBAC					1							3	3
VER009								2				1	2
UNK090						1	2					2	3
ORPULP		1		3		1						3	5
PULP		3		1		37	27	10		4	1	10	95
Species[a]	2	4	2	6	19	63	52	14	3	3	4		
Records[b]	6	14	7	14	44	277	200	55	8	20	10		

Bird species represented by <5 fecal samples. Plant species recorded in fecal samples are in parentheses following the bird species: CFUS (MICAFF, UREBAC); VIOL (CONSUB, PINCOR); VEPI (CONSUB); DFUS (MICAFF); DECA (PULP, CONSUB); HEVE (CLIDEN, CONSUB, MICAFF); PIRU (PULP, CECINS, FICCOL, MICAFF); PIOL (CONSUB, MICAFF, PASAUR); PHLU (PULP); ICGA (UREBAC).

Plant species represented in only 1 fecal sample are listed by bird species from which the samples were obtained: TYTY (PIP007, UNK106); CAMI (CONBRA, NEEPSY, UNK041); CAUS (ANTHUR, ERI252, ALCCOS, DRYPIL, CLU113, MARAFF, CLIEPI, CON162, MIC055, OSSROB, MEL073, MEL118, MEL108, MEL103, SIPTON, PSYGST, SAB094, RUB390, URECAR, CISPSE, UNK046); HYMU (DIEFFE, HELWAG, SMILAX, DILLEN, CLUPAL, CLICRE, MICGRA, MICSER, MICSPP, TOP175, PSY099, LYC084, VITCOO, UN2441, UN0885, UN1641); DUCA (XIPCOE); OPFOR (CLIDIS).

[a] Species = number of plant species recorded in the bird species' diet; pulp records are not included in species total.
[b] Records = number of records of fruit seeds or pulp; total can be larger than number of fecal samples because many fecal samples contain seeds from >1 plant species.

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

TABLE 3. *Number of fecal samples (N), percent with insects (% I), and percent with fruit (% F) collected from migrants in different habitats. Bird species codes in Table 1.*

Habitat	All species			CAMI			CAUS			HYMU		
	N	% I	% F	*N*	% I	% F	*N*	% I	% F	*N*	% I	% F
Young second-growth	475	81	57	16	88	94	100	49	99	62	89	65
Old second-growth	123	83	53	3	100	100	39	54	97	21	90	67
Primary forest												
Lowland (50 m)	158	86	63	3	67	100	27	41	100	115	96	59
Foothill (500 m)	84	87	60				20	70	95	59	92	51
Premontane (1000 m)	24	88	71				13	77	100	2	100	100

Habitat	EMVI			DEPE			SEAU			OPFO		
	N	% I	% F	*N*	% I	% F	*N*	% I	% F	*N*	% I	% F
Young second-growth	13	100	38	32	100	22	72	100	24	54	100	13
Old second-growth	4	100	0	12	100	8	8	100	0	23	100	13
Primary forest (all)	6	100	17							9	100	0

aging behavior (Martin 1985a, Moermond & Denslow 1985). Gape width of the bird affects the size range of fruits that birds consume (Wheelwright 1985) and may influence patterns of habitat selection (Martin 1985b). Most warblers encountered during this study have relatively small gapes and were primarily insectivorous. Many eat fruit infrequently and are perhaps most likely to opportunistically consume small, juicy berries of the Melastomataceae (*e.g., Conostegia subcrustulata* and *Miconia affinis* eaten by Kentucky Warbler and Ovenbird). In contrast, migrant thrushes, mimids, and some flycatchers have larger gapes than warblers and consumed substantial amounts of fruit, often of many different species.

Fruit handling technique also affects the number and types of fruits consumed. Mimids and thrushes commonly swallow fruits whole ("gulpers" of Moermond & Denslow 1985); fruit selection is likely to be constrained by gape size. Birds that mandibulate fruits in their bills ("mashers"; *e.g., Piranga* tanagers), may be less constrained. Although we obtained relatively few samples from such migrants (see Table 2), those samples we did obtain suggest that these birds also feed on a wide variety of fruits.

Many of the species that consumed fruit at La Selva have been reported to consume fruit elsewhere in the tropics (Leck 1972b, Morton 1980, Greenberg 1981, Martin 1985b). Wheelwright *et al.* (1984) presented a survey of fruit use by 70 species of birds at Monteverde, Costa Rica, a mid-elevation site (1350–1550 m). Four species of neotropical migrants were reported to consume 13 (Swainson's Thrush), 4 (Summer Tanager), 4 (Northern Oriole), and 2 (Solitary Vireo *Vireo solitarius*) species of fruits. Number of samples (fecal samples, observations) collected from each species was not presented by Wheelwright *et al.* (1990), so direct comparisons by species with the present study are not possible. Keeping this in mind, we recorded a similar number of fruits in the diet of Summer Tanagers at La Selva (5 species; 6 samples) but found many more species of fruits (63) in the diet of Swainson's Thrush; 52 species were recorded from Wood Thrushes. The species with the greatest diversity of fruits in its diet at Monteverde (95 species) was the Emerald Toucanet (*Aulacorhynchus prasinus*), a permanent resident. Our data thus demonstrate that some migrants may rival permanent residents in the number of fruits consumed. The diversity of fruits in the diets of some migrants suggests that they, like many resident frugivores, may disperse the seeds of many plant species. The relative importance of migrants as seed dispersers will also depend on the probability that seeds are disseminated to suitable sites for survival and growth (Greenberg 1981). Few data are currently available to assess this point.

Although many species may eat fruit throughout the nonbreeding season (*e.g.,* Eastern Kingbird; Morton 1971), temporal shifts in degree of frugivory also occur (Greenberg 1981). Wood Thrushes are more frugivorous during the late dry season (spring) than earlier (winter). A shift to greater frugivory by migrants during the later dry season in Panama has been noted by previous authors (Leck 1972b, Morton 1980, Martin & Karr 1986). Such increases in frugivory likely relate to increased need to accumulate fat for migration (Martin 1985b,

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

Loiselle & Blake 1991). A higher degree of frugivory during migratory periods may have important consequences for seed dispersal; birds may be more likely to move greater distances at this time than during the winter, when many are on winter territories.

Abundant supplies of fruit in many second-growth habitats may be a partial explanation for the use of such habitats by many species of migrants (Martin 1985b), as well as by many permanent residents (Blake & Loiselle 1991). Fruit often is abundant in second-growth habitats throughout the year (Levey 1988, Blake & Loiselle 1991) and may, as a consequence, be an important resource for many animals when fruit abundance is low in forests (Terborgh 1985, Levey 1988, Blake & Loiselle 1991). Many species, including both residents and migrants, move from forest to second-growth during periods when fruit is low in abundance in forests (Martin 1985b, Martin & Karr 1986, Blake & Loiselle 1991).

The adverse consequences to many species of loss of tropical forests has received much attention (*e.g.,* Raven 1988); conversion of second-growth habitats to pasture will have negative effects on many species as well. Effects may be felt not only by second-growth species but also by forest species that use second-growth on a seasonal or irregular basis. Thus, it is appropriate to incorporate consideration of second-growth habitats when discussing strategies for habitat management and species preservation (Gilbert 1980).

ACKNOWLEDGMENTS

We thank the Organization for Tropical Studies for permission to work at La Selva and David and Deborah Clark for facilitating our research there; Servicio de Parques Nacionales, particularly F. Cortes and J. Doblez, for permission to work in Parque Nacional Braulio Carrillo; and Russ Greenberg and an anonymous reviewer for constructive comments on the manuscript. Primary support for this project was provided by: Jessie Smith Noyes Foundation Fellowship (Organization for Tropical Studies); Michael H. Guyer Fellowship (Department of Zoology, University of Wisconsin); National Geographic Society; and the Douroucouli Foundation.

LITERATURE CITED

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Curr. Ornithol. 7: 1–57.

Blake, J. G., and B. A. Loiselle. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. Auk 108: 114–130.

———, and B. A. Loiselle. In press. Habitat use by neotropical migrants at La Selva Biological Station and Braulio Carrillo National Park, Costa Rica. *In* J. Hagan and D. W. Johnston (Eds.). Ecology and conservation of neotropical landbird migrants. Smithsonian Institution Press, Washington, D.C.

———, G. J. Niemi, and J. M. Hanowski. In press. Drought and annual variation in bird populations. *In* J. Hagan and D. W. Johnston (Eds.). Ecology and conservation of neotropical landbird migrants. Smithsonian Institution Press, Washington, D.C.

———, F. G. Stiles, and B. A. Loiselle. 1990. Birds of La Selva: habitat use, trophic composition, and migrants. *In* A. Gentry (Ed.). Four neotropical rain forests, pp. 161–182. Yale University Press, New Haven, Connecticut.

Gilbert, L .E. 1980. Food web organization and the conservation of neotropical diversity. *In* M. E. Soule and B. A. Wilcox (Eds.). Conservation biology, pp. 11–33. Sinauer Associates, Inc., Sunderland, Massachusetts.

Greenberg, R. 1981. Frugivory in some migrant tropical forest wood warblers. Biotropica 13: 215–223.

Hagan, J., and D. W. Johnston (Eds.). In press. Ecology and conservation of neotropical landbird migrants. Smithsonian Institution Press, Washington, D.C.

Hartshorn, G. S. 1983. Plants: introduction. *In* D. H. Janzen (Ed.). Costa Rican natural history, pp. 118–157. University Chicago Press, Chicago, Illinois.

———, and R. Peralta. 1988. Preliminary description of primary forests along the La Selva–Volcan Barva altitudinal transect, Costa Rica. *In* F. Almeda and C. M. Pringle (Eds.). Tropical rain forests: diversity and conservation, pp. 281–296. California Academy of Sciences, San Francisco, California.

Howe, H. F., and D. DeSteven. 1979. Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. Oecologia 39: 185–196.

Hutto, R. L. 1989. The effect of habitat alteration on migratory land birds in a West Mexican tropical deciduous forest: a conservation perspective. Conserv. Biol. 3: 138–148.

Keast, A., and E. S. Morton (Eds.). 1980. Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C.

Leck, C. F. 1972a. Seasonal changes in feeding pressures of fruit- and nectar-eating birds in Panama. Condor 74: 54–60.

———. 1972b. The impact of some North American migrants at fruiting trees in Panama. Auk 89: 842–850.

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

LEVEY, D. J. 1986. Methods of seed processing by birds and seed deposition patterns. *In* A. Estrada and T. H. Fleming (Eds.). Frugivores and seed dispersal, pp. 147–158. Dr. W. Junk, Publishers, Dordrecht, The Netherlands.

———. 1987. Seed size and fruit-handling techniques of avian frugivores. Am. Nat. 129: 471–485.

———. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecol. Monogr. 58: 251–269.

LOISELLE, B. A. 1987a. Birds and plants in a neotropical rain forest: seasonality and interactions. Ph.D. Dissertation, University of Wisconsin, Madison, Wisconsin.

———. 1987b. Migrant abundance in a Costa Rican lowland forest canopy. J. Trop. Ecol. 3: 163–168.

———, AND J. G. BLAKE. 1990. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. Stud. Avian Biol. 13: 91–103.

———, AND ———. 1991. Resource abundance and temporal variation in fruit-eating birds along a wet forest elevational gradient in Costa Rica. Ecology 82: 494–500.

MARTIN, T. E. 1985a. Resource selection by tropical frugivorous birds: integrating multiple interactions. Oecologia 66: 563–573.

———. 1985b. Selection of second-growth woodlands by frugivorous migrating birds in Panama: an effect of fruit size and plant density? J. Trop. Ecol. 1: 157–170.

———, AND J. R. KARR. 1986. Temporal dynamics of neotropical birds with special reference to frugivores in second-growth woods. Wilson Bull. 98: 38–60.

MOERMOND, T. C., AND J. S. DENSLOW. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Ornithol. Monogr. 36: 865–897.

MORTON, E. S. 1971. Food and migration habits of Eastern Kingbirds in Panama. Auk 88: 925–926.

———. 1980. Adaptations to seasonal changes by migrant land birds in the Panama Canal Zone. *In* A. Keast and E. S. Morton (Eds.). Migrant birds in the neotropics: ecology, behavior, distribution, and conservation, pp. 437–453. Smithsonian Institution Press, Washington, D.C.

PRINGLE, C., I. CHACON, M. GRAYUM, H. GREENE, G. HARTSHORN, G. SCHATZ, G. STILES, C. GOMEZ, AND M. RODRIGUEZ. 1984. Natural history observations and ecological evaluation of the La Selva Protection Zone, Costa Rica. Brenesia 22: 189–206.

RAPPOLE, J. H., E. S. MORTON, T. E. LOVEJOY, AND J. L. RUOS. 1983. Nearctic avian migrants in the neotropics. U.S. Department Interior, Fish and Wildlife Service, Washington, D.C.

RAVEN, P. H. 1988. Our diminishing tropical forests. *In* E. O. Wilson (Ed.). Biodiversity, pp. 119–122. National Academy Press, Washington, D.C.

TERBORGH, J. 1985. Five New World primates: a study in comparative ecology. Princeton University Press, Princeton, New Jersey.

———. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey.

WHEELWRIGHT, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66: 808–818.

———, W. A. HABER, K. G. MURRAY, AND C. GUINDON. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica 16: 173–192.

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

APPENDIX. *Plant species recorded in the diets of birds captured in mist nets.*

Family	Species	Code
Araceae		
	Anthurium sp.	ANTHUR
	Dieffenbachia sp.	DIEFFE
Haemodoraceae		
	Xiphidium coeruleum	XIPCOE
Heliconiaceae		
	Heliconia wagneriana	HELWAG
Smilacaceae		
	Smilax sp.	SMILAX
Araliaceae		
	Dendropanax arboreus	DENARB
	Schefflera systyla	SCHSYS
Cecropiaceae		
	Cecropia insignis	CECINS
	C. obtusifolia	CECOBT
Compositae		
	Clibadium asperum	CLIASP
Dilleniaceae		
	Doliocarpus dentatus	DOLDEN
	Pinzona coriacea	PINCOR
	Dilleniaceae sp.	DILLEN
Ericaceae		
	Ericaceae sp.	ERI252
Euphorbiaceae		
	Alchornea costaricensis	ALCCOS
Gesneriaceae		
	Besleria columneoides	BESCOL
	Drymonia pilifera	DRYPIL
Guttiferae		
	Clusia palmana	CLUPAL
	Clusia sp.	CLU113
Lauraceae		
	Nectandra membranacea	NECMEM
Malvaceae		
	Hampea appendiculata	HAMAPP
Marcgraviaceae		
	Marcgravia affinis	MARAFF
Melastomataceae		
	Clidemia crenulata	CLICRE
	C. densiflora	CLIDNS
	C. dentata	CLIDEN
	C. epiphytica	CLIEPI
	C. discolor	CLIDIS
	Conostegia bracteata	CONBRA
	C. subcrustulata	CONSUB
	Conostegia sp.	CON162
	Henriettea tuberculosa	HENTUB
	Leandra sp.	LEANDR
	Miconia affinis	MICAFF
	M. appendiculata	MICAPP
	M. "attenuate"	MICATT
	M. barbinervis	MICBAR
	M. brenesii	MICBRE
	M. centrodesma	MICCEN
	M. gracilis	MICGRA
	M. multispicata	MICMUL
	M. nervosa	MICNER
	M. serrulata	MICSER
	M. simplex	MICSIM
	M. aff. *smaragdina*	MICSMA
	M. sp.	MICSPP
	M. sp.	MIC110
	M. sp.	MIC055
	M. sp.	MIC036
	M. sp.	MIC280
	Ossaea macrophylla	OSSMAC
	O. robusta	OSSROB
	Ossaea sp.	OSSSPP
	Topobea sp.	TOP175
	Melastomataceae sp.	MEL073
	Melastomataceae sp.	MEL118
	Melastomataceae sp.	MEL108
	Melastomataceae sp.	MEL103
Menispermaceae		
	Cissampelos sp.	CISSAM
Monimiaceae		
	Siparuna tonduziana	SIPTON
Moraceae		
	Ficus sp.	FICCOL
Myrsinaceae		
	Ardisia auriculata	AURAUR
	A. nigropunctata	AURNIG
Nyctaginaceae		
	Neea psychotrioides	NEEPSY
Passifloraceae		
	Passiflora auriculata	PASAUR
Phytolaccaceae		
	Phytolacca rivinoides	PHYRIV
	Trichostigma polyandrum	TRIPOL
Piperaceae		
	Piper sp.	PIP007
Rubiaceae		
	Bertiera guianensis	BERGUI
	Cephaelis elata	CEPELA
	Hamelia patens	HAMPAT
	Psychotria brachiata	PSYBRA
	P. copensis	PSYCOP
	P. grandis	PSYGRA
	P. grandistipulata	PSYGST
	P. orchidearum	PSYORC
	P. officinalis	PSYOFF
	P. pittieri	PSYPIT
	P. psychotriifolia	PSYPSY
	Psychotria sp.	PSY099
	Sabicea villosa	SABVIL
	Sabicea sp.	SAB060

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

APPENDIX. *Continued.*

Family/Species	Code	Family/Species	Code
Sabicea sp.	SAB094	Vitaceae	
Rubiaceae sp.	RUB390	*Cissus pseudosicyoides*	CISPSE
Solanaceae		Unknown	
Cestrum racemosum	CESRAC	Unknown sp.	UNK090
Lycianthes sp.	LYC084	Unknown sp.	UNK106
Witheringia asterotricha	WITAST	Unknown sp.	UNK046
Urticaceae		Unknown sp.	UNK041
Urera baccifera	UREBAC	Unknown sp.	UN0855
U. caracasana	URECAR	Unknown sp.	UN1641
Verbenaceae		Unknown sp.	UN2441
		Orange pulp	ORPULP
Vitex cooperi	VITCOO	Juice, pulp (not orange)	PULP
Verbenaceae sp.?	VER009		

This content downloaded from 128.227.179.195 on Wed, 16 Sep 2015 14:57:50 UTC
All use subject to JSTOR Terms and Conditions

View publication stats