

# DIETS OF LAND BIRDS FROM NORTHEASTERN VENEZUELA<sup>1</sup>

BRIGITTE POULIN, GAËTAN LEFEBVRE AND RAYMOND McNEIL

Département de sciences biologiques, Université de Montréal C.P. 6128, succursale centre-ville,  
Montréal, Québec H3C 3J7 Canada

**Abstract.** We estimate diets of 68 bird species inhabiting dry seasonal habitats and mangroves of northeastern Venezuela, based on 3,419 birds forced to regurgitate using tartar emetic. Most birds were generalist feeders, including a wide variety of both invertebrate and plant taxa in their diet. Coleopterans, ants, and insect larvae were the most frequent invertebrate preys. Hummingbirds had low nectar intakes and differed from other species by feeding extensively on small soft-bodied arthropods. Most species fed on fruits to a variable extent. Actually, several species tended to be more frugivorous at our study sites than in previous reports.

**Key words:** *Arid habitats; diet; mangroves; Venezuela.*

## INTRODUCTION

Direct examination of diets is generally under-represented in studies of avian ecology (Rosenberg and Cooper 1990). In particular, the diet of many neotropical species is poorly known (Collins et al. 1990, Karr and Brawn 1990, Loiselle and Blake 1990). Food exploitation is nevertheless central to our understanding of avian community organization. Many studies carried out in tropical latitudes have related bird abundance and phenology to feeding habits (e.g., Snow and Snow 1964, Orians 1969, Karr 1976, Greenberg 1981, Bell 1982, Wong 1986, Loiselle 1988). In most cases, species were assigned to feeding guilds using taxonomy, individual observations, or data drawn from the literature. Information on diets was slight and collected during a small portion of the annual cycle.

Here we estimate the diet of 68 bird species found in the major habitats of northeastern Venezuela (i.e., thorn scrub, thorn woodland, thorn forest, deciduous forest, and mangrove woodlands) (Sarmiento 1976). Diet samples were obtained twice monthly over two annual cycles by forcing 3,419 birds to regurgitate using antimony potassium tartrate (Poulin et al. 1994).

## METHODS

This study was carried out in Guarapo (10°39'00"N, 63°41'55"W) and Laguna de Cocos (10°29'33"N, 63°45'00"W) on the Araya Peninsula, in the state of Sucre, northeastern Ven-

zuela. In Guarapo, three study areas were delimited within 7 km along a humidity gradient from the coast to inland areas and correspond to a thorn scrub, a thorn woodland, and a deciduous forest (Sarmiento 1972, 1976). In Laguna de Cocos, sampling was done in a thorn forest and in black mangrove (*Avicennia germinans*) woodland.

At all study sites, birds were mist-netted twice monthly during at least a complete annual cycle between September 1984 and August 1987. Regurgitation samples were obtained by administering tartar emetic to wild-caught birds (see Poulin et al. [1994] for details of methodology). Food items were identified to order or family (invertebrates) or to species (fleshy fruits). Dry fruits were counted when possible and assigned to species, but most of them were not identified taxonomically. Because nectar is 100% assimilable (Remsen et al. 1986), its consumption was evaluated through the presence of pollen grains in emetic samples.

## RESULTS

### SPECIES DIET

The intake of invertebrate and plant food is detailed for each species in Appendices 1 and 2, respectively. Although not appearing in the tables, we found a fish in a sample of the kingfisher *Chloroceryle americana*. We do not have samples from carnivorous species, but on three occasions in mangroves an owl (*Glaucidium brasilianum*) was captured along with its prey: a cicada, a bat, and a passerine (*Conirostrum bicolor*).

Diets of the most abundant species are summarized below by grouping the species that fed

<sup>1</sup> Received 9 November 1993. Accepted 15 November 1993.

regularly on specific food types, i.e., nectar, insects, fruits, and seeds.

In most nectarivorous species, the proportion of samples with pollen was inversely related to arthropod intake (Appendices 1 and 2), suggesting that the presence of pollen reflects a reasonable overall estimate of nectar consumption. With the exception of *Glaucois hirsuta* that showed a clear preference for nectar, most hummingbirds fed extensively on small, soft-bodied arthropods. As many as 8.8 and 6.5 arthropods were identified on average in *Amazilia tobaci* and *Leucippus fallax*, the two most abundant species. Hummingbirds differed from other species by feeding mainly on small Diptera, wasps, and spiders, whereas only *Leucippus fallax* fed consistently on Coleoptera. Some hummingbirds occasionally fed on seeds and fleshy fruits. These were probably not taken accidentally, since 24 seeds were found in a single sample from *Amazilia tobaci*. Among passerines, *Coereba flaveola* included in a wide range of resources among nectar, fruits, seeds, and invertebrates, with insect larvae the most important prey in the last category.

Among insectivores, *Hypnelus ruficollis* and *Thamnophilus dolius* fed on a great variety of large invertebrates. Woodcreepers (*Xiphorhynchus* and *Lepidocolaptes*) fed mainly on non-flying arthropods. *Formicivora grisea* was an opportunistic feeder as suggested by the high number of taxa taken (Table 1), as well as its consumption of winged ants and termites. *Atalotriccus pilaris*, also fed on a wide variety of invertebrate taxa, but mostly on small Coleoptera. Feeding generalism was particularly notable in mangroves where both residents (*Conirostrum bicolor*, *Certhiaxis cinnamomea*, *Fluvicola pica*) and nearctic migrants (*Seiurus noveboracensis*, *Protonotaria citrea*, *Setophaga ruticilla*) included an impressive number of invertebrate taxa in their diet relative to the number of emetic samples (Table 1). Few insectivores specialized on specific taxa, but *Sublegatus modestus* showed a clear preference for ants which accounted for 80% of all arthropods taken.

Some small frugivorous-insectivorous species, such as *Phaeomyias murina* and *Hylophilus flavipes*, included a large diversity of plant species as well as arthropod taxa in their diet (Table 1). *Tachyfonus rufus* fed extensively on fruits from several species, but showed a clear preference for large ants among invertebrates. *Mimus gilvus* was another highly frugivorous species with an av-

erage of 17 fruits (1,684/100) per emetic sample, taken from 18 different plant species. This mockingbird nevertheless fed on a wide variety of invertebrates, mainly large ground-dwelling arthropods. *Thraupis glaucocolpa* was characterized by a lower intake of arthropod compared to other mixed-feeders (Table 1). Among the Tyrannidae, *Elaenia parvirostris*, *Phaeomyias murina* and *Myiarchus tyrannulus* were the most frugivorous. The Dendrocolaptidae and Formicariidae also fed on fruits, but to a lesser extent.

Two unidentified dry fruit species were taken by 15 bird species, although only *Tiaris bicolor* and *Coryphospingus pileatus* can be considered granivores. *Tiaris bicolor* alone fed on seeds from 13 different species, whereas arthropods (mainly insect larvae, Homoptera, Coleoptera, and Isoptera) were observed in only 23% of the samples. *Coryphospingus pileatus* fed more regularly on insects, especially Coleoptera and ants.

#### FOOD EXPLOITATION AT THE COMMUNITY LEVEL

The number of species feeding on specific invertebrate taxa was highest for Coleoptera (52), ants (45), insect larvae (44), spiders (37), and wasps (35) (Table 2). Most birds represented by large sample size fed on several invertebrate taxa, but still showed a clear preference for Coleoptera and Hymenoptera (ants) (Table 2). These two invertebrate taxa alone accounted for 60% of all invertebrate items found in emetic samples and represented the first- and second-most important prey for 32 and 22 birds species, respectively (Table 2). Actually, species feeding more extensively on other invertebrate taxa were mostly hummingbirds (Diptera, wasps, Araneae) and mangrove species (Homoptera, Lepidoptera).

The mean number of items within a sample varied according to the different invertebrate taxa (Fig. 1). Large invertebrates, such as isopods, millipedes, centipedes, scorpions, dragonflies, and orthopterans tended to be represented by a single item in samples. Many of the most frequent taxa in the birds' diet such as Coleoptera, insect larvae, wasps, and spiders were represented by only two or three items on average per sample. Diptera and ants tended to be represented by four or five items. Finally, termites, winged ants, and insect eggs all occurred in high numbers within a same sample.

Most birds also fed on vegetable matter to a variable extent. Of 68 bird species, only 21 never

TABLE 1. Occurrence and diversity of the different food types in the diet of the bird species represented by more than five emetic samples.

Bird species	Number of samples	Percent of emetic samples with				Number of taxa taken		
		Invertebrates	Fleshy fruits	Seeds <sup>1</sup>	Pollen	Invertebrates	Fleshy fruits	Seeds
<i>Glaucis hirsuta</i>	8	38			100	4	0	0
<i>Chlorostilbon mellisugus</i>	42	86			50	6	0	0
<i>Leucippus fallax</i>	121	91	2		55	11	1	3
<i>Amazilia tobaci</i>	48	96		4	33	9	0	1
<i>Hypnelus ruficollis</i>	8	88	13			9	1	0
<i>Melanerpes rubricapillus</i>	9	89	67			3	6	0
<i>Certhiaxis cinnamomea</i> <sup>2</sup>	17	100				12	0	0
<i>Xiphorhynchus picus</i>	24	100		4		8	0	1
<i>Lepidocolaptes souleyetii</i> <sup>2</sup>	17	100	6			10	1	0
<i>Thamnophilus doliatus</i>	27	100	11			12	0	0
<i>Formicivora grisea</i>	114	99	2	1		16	2	1
<i>Phaeomyias murina</i>	153	82	81	1		13	19	1
<i>Sublegatus modestus</i>	139	100	19	3		11	9	2
<i>Myiopagis viridicata</i>	6	100	17			5	2	0
<i>Elaenia parvirostris</i>	14	50	93			3	7	0
<i>Atalotriccus pilaris</i>	124	99	10	4		15	6	4
<i>Idioptilon margaritaceiventris</i>	6	100	17			6	2	0
<i>Tolmomyias flaviventris</i> <sup>2</sup>	12	100	8	8		7	1	1
<i>Cnemotriccus fuscatus</i>	25	100	12	4		8	3	1
<i>Fluvicola pica</i> <sup>2</sup>	19	100				11	0	0
<i>Myiarchus tyrannulus</i>	37	84	51	3		10	12	1
<i>Troglodytes aedon</i>	8	100				8	0	0
<i>Polioptila plumbea</i>	80	99	3	4		11	1	2
<i>Mimus gilvus</i>	100	67	91	1		10	18	2
<i>Vireo olivaceus</i>	45	98	27	2		13	6	0
<i>Hylophilus flavipes</i>	125	85	83	4		13	14	3
<i>Setophaga ruticilla</i> <sup>2</sup>	15	100				11	0	0
<i>Protonotaria citrea</i> <sup>2</sup>	34	97	3			10	1	0
<i>Seiurus noveboracensis</i> <sup>2</sup>	98	100				16	0	0
<i>Coereba flaveola</i>	503	85	12	3	64	11	8	6
<i>Conirostrum bicolor</i> <sup>2</sup>	118	100	1			14	1	0
<i>Thraupis glaucocolpa</i>	40	20	100			3	11	0
<i>Tachyfonus rufus</i>	71	93	80	6		7	13	2
<i>Coryphospingus pileatus</i>	113	75	5	59		8	4	8
<i>Cardinalis phoeniceus</i>	80	83	48	84		6	10	6
<i>Sporophila lineola</i>	6			100		0	0	2
<i>Tiaris bicolor</i>	231	23	8	95		10	5	13
<i>Icterus nigrogularis</i>	9		22			7	3	0

<sup>1</sup> Refers either to dry fruits or to fleshy fruits whose seeds were pounded in samples.<sup>2</sup> Species mostly or entirely sampled in mangrove habitat.

fed on plant food. Of these, 17 species were represented by three emetic samples or less, and three were species occupying mangrove areas (mangrove fruit pods are not consumed by passerines, Smith 1987). *Tournefortia scandeus*, *Lycium nodosum*, and *Pilosocereus moritzianus* were the most important fruits in the birds' diet (Table 3). Fruits from many plant species were taken by several bird species, but each bird species tended to have its own preferred fruit (Table 3). Although *Tournefortia scandeus* was the most important fruit in the birds' diet in terms of emetic samples as well as number of bird species, it was

the first choice of only two species, both insectivorous (*Sublegatus modestus* and *Atalotriccus pilaris*). On the other hand, *Lycium nodosum* was the preferred fruit of two highly frugivorous species (*Mimus gilvus* and *Elaenia parvirostris*). Although fruits of *Erythroxylum cumanense* were taken by 15 bird species, only *Tachyfonus rufus* fed extensively on them. *Erythroxylum* sp., on the contrary, was the preferred fruit of three small mixed-feeders but overall was taken by four bird species only. The same pattern was observed for *Trichilia trifoliata*. Granivores, such as *Tiaris bicolor* and *Coryphospingus pileatus*, showed a clear

TABLE 2. Importance of the different invertebrate taxa in the birds' diet.

Taxa	Invertebrate intake			Number of bird species	
	Number of items	Number of emetic samples	Number of bird species	First choice <sup>1</sup>	Second choice
Gastropoda	51	34	12		
Decapoda; crabs	17	12	4		
Isopoda	6	6	3		
Scorpionoidea	3	3	3		
Araneae	410	173	37	1	2
Ixodidae (ticks)	6	6	6		
Diplopoda (millipedes)	15	13	6		
Chilopoda (centipedes)	3	3	2		
Odonata	12	10	8		
Orthoptera	45	34	14		
Isoptera	221	19	13	1	
Psocoptera	3	2	2		
Hemiptera	187	118	28		
Homoptera	257	127	25	1	2
Neuroptera	2	2	1		
Coleoptera	3,218	1,127	52	22	10
Lepidoptera	78	54	17		1
Diptera	613	150	23	3	2
Hymenoptera; ants	3,150	664	45	10	11
Hymenoptera; winged ants	215	30	11		
Hymenoptera; wasps	690	250	35	1	3
Insect eggs	250	44	11	1	1
Insect pupae	15	13	6		
Insect larvae	1,064	360	44	3	11

<sup>1</sup> Based on the number of invertebrates taken by species that fed on at least 10 invertebrate items.

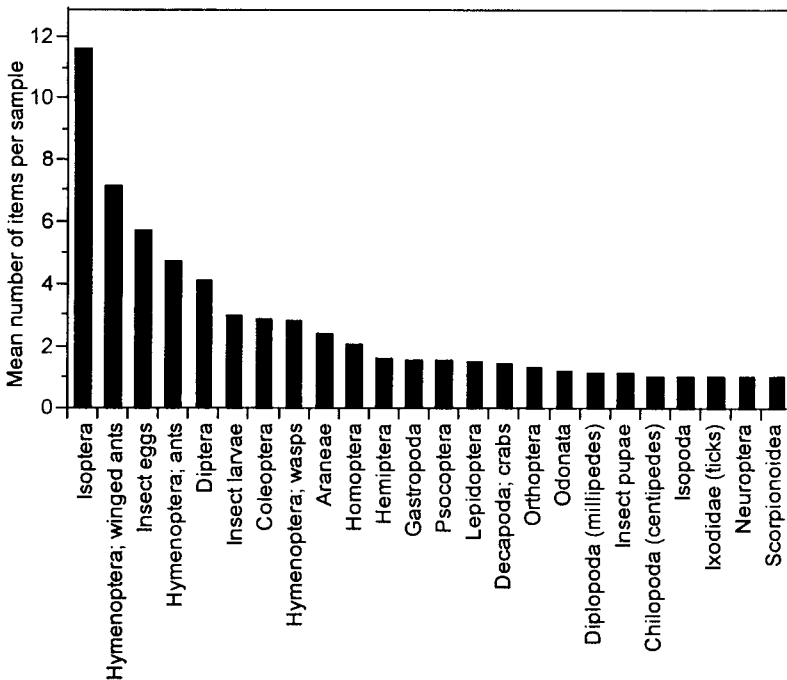


FIGURE 1. Mean number of items per emetic sample for each invertebrate taxa.

TABLE 3. Importance of the different fruit species in the birds' diet.

Plant species	Fruit intake		Number of bird species	
	Number of emetic samples	Number of bird species	First choice <sup>1</sup>	Second choice
<b>Acanthaceae</b>				
<i>Ruella tuberosa</i>	1	1		
<b>Boraginaceae</b>				
<i>Tournefortia scandens</i>	96	16	2	2
<i>Cordia curassavica</i>	4	3		
<b>Bromeliaceae</b>				
<i>Bromelia pinguin</i>	40	6	1	
<b>Burseraceae</b>				
<i>Bursera karsteniana</i>	19	6		
<b>Cactaceae</b>				
<i>Subpilocereus</i> sp.	8	2		
<i>Acanthocereus tetragonus</i>	4	2		
<i>Pilosocereus moritzianus</i>	69	13	3	1
<i>Opuntia</i> <sup>2</sup>	3	3		
<i>Melocactus caesius</i>	52	9	1	2
<b>Capparidaceae</b>				
<i>Capparis odoratissima</i>	58	9	2	1
<b>Cucurbitaceae</b>				
<i>Doyerea emetocartartica</i>	51	6		
<b>Erythroxylaceae</b>				
<i>Erythroxylum cumanense</i>	53	15		1
<i>Erythroxylum</i> sp.	58	4	1	1
<b>Euphorbiaceae</b>				
<i>Croton rhamnifolius</i>	4	2		
<b>Flacourtiaceae</b>				
<i>Casearia sylvestris</i>	1	1		
<b>Leguminosae</b>				
<i>Pithecellobium oblongum</i>	4	3		
<b>Malpighiaceae</b>				
<i>Malpighia glabra</i>	1	1		
<b>Malvaceae</b>				
<i>Gossypium hirsutum</i>	3	2		
<i>Sida acuta</i>	1	1		
<i>Trichilia trifoliata</i>	46	5	1	1
<b>Nyctaginaceae</b>				
<i>Guapira microfila</i>	18	8		
<b>Rutaceae</b>				
<i>Zanthoxylon pterota</i>	34	11		
<b>Simarubaceae</b>				
<i>Castela erecta</i>	2	1		
<b>Solanaceae</b>				
<i>Solanum gardneri</i>	4	3		
<i>Lycium nodosum</i>	78	18	3	2
<i>Capsicum</i> sp.	2	2		
<i>Solanum agrarium</i>	20	10		
<b>Theophrastaceae</b>				
<i>Jacquinia revoluta</i>	25	5	1	
Unidentified (seven species <sup>3</sup> )	70	22	1	

<sup>1</sup> Based on the number of samples from the bird species that fed on fruits on at least five occasions.

<sup>2</sup> *Opuntia caracasana* and *Opuntia elatior*.

preference for Cactaceae (*Pilocereus* and *Melocactus*) among fleshy fruits. Fruits from *Capparis odoratissima* were taken by several species from different size and food habits. Fruits from *Bromelia pinguin* were taken by large birds only. All other identified fruit species accounted for less than 20% of fruit intake.

## DISCUSSION

Few quantitative data exists on the importance of nectar, arthropods, and fruits in the diets of nectarivores (Collins et al. 1990). Among the most unexpected results was the intake of dry and fleshy fruits by hummingbirds. Fruits might be even more important in their diet since these birds also extract juice from the pulp of cactus fruits (Lack 1976, Wendelken and Martin 1988). Hummingbirds were also characterized by a large amount of soft-bodied arthropods in their diet. Indications of hummingbirds feeding on arthropods are accumulating (Wolf 1970, Young 1971, Leck 1972, Snow and Snow 1972, DesGranges 1979, Mobb 1979, Montgomerie and Redsell 1980, Remsen et al. 1986, Baltosser 1989). Our results agree with those of Remsen et al. (1986) suggesting that arthropod intake by hummingbirds is particularly frequent in arid regions.

Most insectivorous species abundant at our study sites fed on a variety of arthropod taxa, suggesting that dietary specialization of insectivores is not prevalent in tropical dry habitats. The high frequency of Coleoptera, Hymenoptera, insect larvae, and Aranaea in the diets of many species most likely reflects diet opportunism. Sampling of arthropods through different methods (Poulin et al. 1992) showed that Coleoptera was the most abundant taxa in both light traps and sweep-net samples. Ants were the first and third-most abundant taxa in pitfall traps and sweep-net, respectively. Spiders were the second-most important taxa in sweep-net and pitfall traps. Finally, wasps were the third-most important taxa in both light-traps and Malaise traps. Only insect larvae did not follow this trend. Although being the second-most important invertebrate prey in the birds' diet, they accounted for less than 5% of all arthropods sampled by sweep-net. Actually, insect larvae were abundant only during a two-month period that corresponded to the birds' breeding season. Consequently, most birds fed opportunistically on Coleoptera and Formicidae year-round, but showed a clear preference for larvae during breeding activity. The

predominance of coleopterans, ants, larvae, and spiders also suggests that most bird species foraged by gleaning. In arid habitats, only hummingbirds and *Myiarchus tyrannulus* were occasionally observed hawking or flycatching for their prey. In mangroves, however, several species regularly caught their prey on the wing.

Frugivory has been reported for many tropical species, but most studies relate to birds feeding at individual fruiting trees. Several of our species feeding extensively on fleshy fruits such as *Mimus gilvus*, *Tachyfonus rufus*, *Phaeomyias murina*, and the genera *Thraupis* and *Elaenia* are recognized as mainly frugivorous (Haverschmidt 1968, Snow and Snow 1971, Traylor and Fitzpatrick 1981, Scott and Martin 1984, Belton 1985, Moermond and Denslow 1985). Partial frugivory has also previously been observed for *Amazilia*, *Melanerpes*, *Camptostoma*, *Sublegatus*, *Myiopagis*, *Myiarchus*, *Pitangus*, *Myiozetetes*, *Vireo*, *Protonotaria*, *Molothrus*, and *Icterus* (Diamond and Terborgh 1967; Haverschmidt 1968; Leck 1971, 1972; Cruz 1974; Howe 1977; Morton 1977; Traylor and Fitzpatrick 1981; Scott and Martin 1984; Trainer and Will 1984; Belton 1985; Moermond and Denslow 1985; Foster 1987; Wendelken and Martin 1988). Intake of fleshy fruits by Formicariidae, an insectivorous tropical family, had previously been noted for *Thamnophilus doliatus* (Haverschmidt 1968, Morton 1973, Keeler-Wolf 1986), as well as *Sakesphorus* and *Pernostola* (Haverschmidt 1968), but this is the first report for *Formicivora*. Among Dendrocolaptidae, another typically insectivorous tropical family, we provide the first report of fruit intake by *Lepidocolaptes* and *Xiphorhynchus*. Neither we could find previous reports of fruit intake by *Leucippus* (Trochilidae), *Hypnelus* (Bucconidae), *Polioptila* (Sylviinae), and *Conirostrum* (Thraupinae). Because *Conirostrum bicolor* was captured in mangroves only, its consumption of fruit implies occasional movements to adjacent thorn forest. The Bananaquit (*Coereba flaveola*), a species of diverse feeding habits (Skutch 1954, Gross 1958, Snow and Snow 1971, Leck 1971, Cruz 1974, Feinsinger et al. 1985), fed more frequently on fleshy fruits at our study sites than in previous reports. The same holds for *Hylophilus flavipes* that fed extensively on fleshy fruits and for which few reports of frugivory exist (Morton 1973). Our results also demonstrate that several members of the Tyrannidae known as primarily insectivorous such as *Atalo-*

*triccus*, *Idioptilon*, *Euscarthmus*, *Tolmomyias*, *Cnemotriccus* and *Contopus* regularly fed on fruits. Our study sites were located in a semiarid region with considerable variation in rainfall and food abundance over the year (Lefebvre 1992, Poulin et al. 1992), and the intake of vegetable matter by many species occurred predominantly during the dry season when arthropod abundance was lowest. In seasonal arid habitat on the Yucatan Peninsula, Lopez Ornat and Lynch (1990) also noted that most birds were generalist feeders depending extensively on vegetable food.

Although some plants were clearly more important in the overall bird diet, fruit preferences varied among the different bird species. Fruit choice was probably a combination of several factors, including the bird and fruit morphology, as well as their respective seasonality. For instance, fruit production of *Lycium nodosum*, a species taken by 18 bird species, occurred in the early dry season when arthropod abundance was low and few plant species were fruiting.

In seasonal habitats of northeastern Venezuela, most species fed on a wide variety of resources, including both vegetal and animal foods in their diet. While the most frugivorous species included arthropods in their diets, several typically insectivorous species fed at least occasionally on fruits. Indeed, food exploitation by many species was quite variable over time (Poulin et al. 1992), as well as between habitats (Poulin et al., in press). We believe that many land birds show more feeding plasticity than is generally assumed, increasing the need for local dietary studies.

#### ACKNOWLEDGMENTS

This study was supported by the Natural Sciences and Engineering Research Council of Canada, Fonds F.C.A.R. (Gouvernement du Québec), and the Université de Montréal. We are also grateful to colleagues of the Universidad de Oriente, in particular Luis José Cumaná for his invaluable assistance in identifying plant specimens and José Ramón Rodríguez S. who was responsible with Raymond McNeil for the collaborative agreement between both universities.

#### LITERATURE CITED

- AOU. 1983. Check-list of North American birds. 6th ed. American Ornithologists' Union, Washington, DC.
- BALTOSSE, W. H. 1989. Nectar availability and habitat selection by hummingbirds in Guadalupe Canyon. *Wilson Bull.* 101:559-578.
- BELL, H. L. 1982. A bird community of lowland forest in New Guinea. 2. Seasonality. *Emu* 82:65-74.
- BELTON, W. 1985. Birds of Rio Grande do Sul Brazil. Part 2. Formicariidae through Corvidae. *Bull. Am. Mus. Nat. Hist.* 180:1-241.
- COLLINS, B. G., J. GREY, AND S. MCNEE. 1990. Foraging and nectar use in nectarivorous bird communities. *Stud. Avian Biol.* 13:110-121.
- CRUZ, A. 1974. Feeding assemblages of Jamaican birds. *Condor* 76:103-107.
- DIAMOND, J. M., AND J. W. TERBORGH. 1967. Observations on bird distribution and feeding assemblages along the rio Callaria, Department of Loreto, Peru. *Wilson Bull.* 79:273-282.
- DESGRANGES, J.-L. 1979. Organization of a tropical nectar-feeding bird guild in a variable environment. *Living Bird* 17:199-236.
- FEINSINGER, P., L. A. SWARM, AND J. A. WOLFE. 1985. Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. *Ecol. Monogr.* 55:1-28.
- FOSTER, M. S. 1987. Feeding methods and efficiencies of selected frugivorous birds. *Condor* 89:566-580.
- GREENBERG, R. 1981. The abundance and seasonality of forest canopy birds on Barro Colorado Island, Panama. *Biotropica* 13:241-251.
- GROSS, A. O. 1958. Life history of the Bananaquit of Tobago island. *Wilson Bull.* 70:257-279.
- HAVERSCHMIDT, F. 1968. Birds of Surinam. Oliver & Boyd, London.
- HOWE, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58:539-550.
- HOYOS, F. J. 1985. Flora de la Isla de Margarita. Monografía no. 34, Sociedad y Fundación La Salle de Ciencias Naturales, Caracas.
- KARR, J. R. 1976. Seasonality, resource availability, and community diversity in tropical bird communities. *Am. Nat.* 110:973-994.
- KARR, J. R., AND J. D. BRAUN. 1990. Food resources of understory birds in central Panama: quantification and effects on avian populations. *Stud. Avian Biol.* 13:58-64.
- KEELER-WOLF, T. 1986. The Barred Antshrike (*Thamnophilus doliatus*) on Trinidad and Tobago: habitat niche expansion of a generalist forager. *Oecologia* 70:309-317.
- LACK, D. 1976. Island biology, illustrated by the land birds of Jamaica. Univ. of California Press, Berkeley.
- LECK, C. F. 1971. Overlap in the diet of some neotropical birds. *Living Bird* 10:89-106.
- LECK, C. F. 1972. Observations of birds at *Cecropia* trees in Puerto Rico. *Wilson Bull.* 84:498-500.
- LEFEBVRE, G. 1992. Dynamique temporelle et spatiale de l'avifaune migratrice et résidente des mangroves côtières du Venezuela. Thèse de Doctorat (Ph.D.), Université de Montréal, Montréal.
- LOISELLE, B. A. 1988. Bird abundance and seasonality in a Costa Rican lowland forest canopy. *Condor* 90:761-772.
- LOISELLE, B. A., AND J. G. BLAKE. 1990. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. *Stud. Avian Biol.* 13:91-103.
- LOPEZ ORNAT, A., AND J. F. LYNCH. 1990. Landbird communities of the coastal dune scrub in the Yucatan Peninsula: species composition, ecology, and

- zoogeographic affinities. *Vida Silvestre Neotropical* 2:21-31.
- MOBB, S. 1979. Methods used by Trochilidae (hummingbirds) when capturing insects. *Aviculture Mag.* 85:26-30.
- MOERMOND, T. C., AND J. S. DENSLOW. 1985. Neotropical frugivores: patterns of behavior, morphology and nutrition, with consequences for fruit selection, p. 865-897. *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and N. G. Smith [eds.], *Neotropical ornithology*. Ornithol. Monogr. No. 36. American Ornithologists' Union, Washington, DC.
- MONTGOMERIE, R. D., AND C. A. REDSELL. 1980. A nesting hummingbird feeding solely on arthropods. *Condor* 82:463-464.
- MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *Am. Nat.* 107:8-21.
- MORTON, E. S. 1977. Intratropical migration in the Yellow-green Vireo and Piratic Flycatcher. *Auk* 94:97-106.
- ORIAN, G. H. 1969. The number of bird species in some neotropical forest. *Ecology* 50:783-796.
- PHELPS, W. H., AND R. MEYER DE SCHAUENSEE. 1979. Una guía de las aves de Venezuela. Princeton Univ. Press, Princeton, NJ.
- POULIN, B., G. LEFEBVRE, AND R. McNEIL. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73: 2295-2309.
- POULIN, B., G. LEFEBVRE, AND R. McNEIL. In press. Characteristics of feeding guilds and variation in diets of bird species of three adjacent tropical sites. *Biotropica*.
- POULIN, B., G. LEFEBVRE, AND R. McNEIL. 1994. Effect and efficiency of tartar emetic in determining the diet of tropical land birds. *Condor* 96:98-104.
- REMSEN, J. V., F. G. STILES, AND P. E. SCOTT. 1986. Frequency of arthropods in stomachs of tropical hummingbirds. *Auk* 103:436-444.
- ROSENBERG, K. V., AND R. J. COOPER. 1990. Approaches to avian diet analysis. *Stud. Avian Biol.* 13:80-90.
- SARMIENTO, G. 1972. Ecological and floristic convergence between seasonal plant formation of tropical and subtropical South America. *J. Ecol.* 60:367-410.
- SARMIENTO, G. 1976. Evolution of arid vegetation in tropical America, p. 65-99. *In* D. W. Goodall [ed.], *Evolution of desert biota*. Univ. of Texas Press, Austin, TX.
- SCOTT, P. E., AND R. F. MARTIN. 1984. Avian consumption of *Bursera*, *Ficus*, and *Ehretia* fruit in Yucatan. *Biotropica* 16:319-323.
- SKUTCH, A. F. 1954. Life histories of Central American birds. Pacific Coast Avifauna, No. 31. Cooper Ornithological Society, Berkeley, CA.
- SMITH, T. J., III. 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology* 68:266-273.
- SNOW, B. K., AND D. W. SNOW. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* 88:291-322.
- SNOW, B. K., AND D. W. SNOW. 1972. Feeding niches of hummingbirds in a Trinidad valley. *J. Anim. Ecol.* 41:471-485.
- SNOW, D. W., AND B. K. SNOW. 1964. Breeding seasons and annual cycles of Trinidad land-birds. *Zoologica (New York)* 49:1-39.
- TRAINER, J. M., AND T. C. WILL. 1984. Avian methods of feeding on *Bursera simaruba* (Burseraceae) fruits in Panama. *Auk* 101:193-195.
- TRAYLOR, M. A., JR., AND J. W. FITZPATRICK. 1981. A survey of the tyrant flycatchers. *Living Bird* 19: 7-50.
- TRUJILLO, B., AND M. PONCE. 1988. Lista inventario de Cactaceae silvestres en Venezuela con sinonimia y otros aspectos relacionados. *Ernstia* 47:1-20.
- WENDELKEN, P. W., AND R. F. MARTIN. 1988. Avian consumption of the fruit of the cacti *Stenocereus eichlamii* and *Pilocereus maxonii* in Guatemala. *Am. Midl. Nat.* 119:235-243.
- WOLF, L. L. 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds. *Condor* 72:1-14.
- WONG, M. 1986. Trophic organization of understory bird in a Malaysian dipterocarp forest. *Auk* 103: 100-116.
- YOUNG, A. M. 1971. Foraging for insects by a tropical hummingbird. *Condor* 73:36-45.



APPENDIX 1. Number of items taken from each invertebrate category by each bird species.

Bird species <sup>1</sup>	Number of invertebrate items (size in mm)													
	Gas- tro- poda (0-10)	Deca- poda; crabs (0-10)	Iso- poda (5-10)	Scor- pion- oidea (5-30)	Ara- neae (0-5)	Ara- neae (5-15)	Ixodi- dae (0-5)	Diplo- poda (>20)	Chilo- poda (10- 25)	Odo- nata (10- 25)	Or- thop- tera (0-5)	Or- thop- tera (5-25)	Isop- tera (5-15)	Pso- cop- tera (0-5)
<i>Coccyzus melacoryphus</i>														
<i>Glaucis hirsuta</i>					1	1					1			
<i>Chrysolampis mosquitus</i>					3	1								
<i>Chlorostilbon mellisugus</i>					25	1								
<i>Thalurania furcata</i>														
<i>Leucippus fallax</i>					110	5								1
<i>Amazilia chionopectus</i>					5	2								
<i>Amazilia fimbriata</i>														
<i>Amazilia tobaci</i>					74	4								2
<i>Hypnelus ruficollis</i>						2				1			1	
<i>Galbula ruficauda</i>														
<i>Melanerpes rubricapillus</i>														
<i>Synallaxis albescens</i>														
<i>Certhiaxis cinnamomea</i>		1			27				1		4		1	
<i>Xiphorhynchus picus</i>	1			1				1						
<i>Lepidocolaptes souleyetii</i>		1		1	1	2		1			3	118		
<i>Campylorhamphus trochilirostris</i>														
<i>Thamnophilus doliatus</i>	1				1		1	1			1			
<i>Formicivora grisea</i>	2		2		1	2		2			2		71	
<i>Myrmeciza longipes</i>														
<i>Camptostoma obsoletum</i>														
<i>Phaeomyias murina</i>						1					1			3
<i>Sublegatus modestus</i>	1				3			1						
<i>Myiopagis viridicata</i>						2								
<i>Elaenia parvirostris</i>														
<i>Euscarthmus meloryphus</i>														
<i>Mionectes oleagineus</i>						1								
<i>Atalotriccus pilaris</i>					1		1			2				2
<i>Idioptilon margaritaceiventris</i>					1									
<i>Tolmomyias flaviventris</i>					1	4								
<i>Cnemotriccus fuscatus</i>					1	1		2					1	
<i>Myiophobus fasciatus</i>														
<i>Fluvicola pica</i>					9					3	1			
<i>Myiarchus tyrannulus</i>	2		1		1	1								
<i>Myiarchus venezuelensis</i>														
<i>Pitangus sulphuratus</i>			1		1									
<i>Myiozetetes similis</i>														
<i>Stelgidopteryx ruficollis</i>														
<i>Troglodytes aedon</i>	1				1				1					
<i>Polioptila plumbea</i>					2									1
<i>Turdus leucomelas</i>					1									
<i>Turdus nudigensis</i>														
<i>Mimus gilvus</i>	1							8						1
<i>Vireo gilvus</i>														
<i>Vireo olivaceus</i>						1			1		1		5	
<i>Hylophilus flavipes</i>				1		1					2			
<i>Cyclarhis gujanensis</i>														
<i>Parula pitiayumi</i>														
<i>Dendroica petechia</i>														
<i>Dendroica striata</i>														
<i>Setophaga ruticilla</i>					2				1	3				
<i>Protonotaria citrea</i>					8	1						1		
<i>Seriurus noveboracensis</i>	35	14			29	9			2	10	6		3	
<i>Coereba flaveola</i>					13	3	1				2			
<i>Conirostrum bicolor</i>	2		3		26	4	1					7		

APPENDIX 1. Extended.

Number of invertebrate items (size in mm)																				
He- mip- tera (0-5)	He- mip- tera (5- 25)	Ho- mop- tera (0-5)	Ho- mop- tera (5- 30)	Neu- rop- tera (10- 15)	Cole- op- tera (0-5)	Cole- op- tera (5- 20)	Lepi- dop- tera (0-5)	Lepi- dop- tera (5- 20)	Dip- tera (0-5)	Dip- tera (5-25)	Hyme- noptera; ants (0-5)	Hyme- noptera; ants (5-20)	Hyme- nop- tera; winged ants (0-10)	Hyme- noptera; wasps (0-5)	Hyme- nop- tera; wasps (5-15)	Insect eggs (0-5)	Insect pupae (0-10)	Insect larvae (0-5)	Insect larvae (5-30)	
						1													1	
						2				34	2				1			1		
										11					1					
2		12			106	1	1			330	3	7		2	236	2		5	1	
			12			22	1	5	2	161	4	2			183	3		6	1	
	4			1		1	9									2		1	7	
						9	1					158	20						3	
2		18	2		10	2	4	5	2		41							20	2	
					34	40					3	15				1		1	30	
					19	16					28	19				7	2		6	
					1	1		3			2	3								
7	2	1	1		33	17		1			18	49			4				1	
	19	18	5		279	16	2	4	3	2	179	85	94	2	8		1	4	32	
					5	4					3									
											7						20		10	
	7	1			236	7		1	2	1	62	14	2	15	12		1	8	42	
4	4	1			185	48		1			944	358	52	5	12				12	
					5	1					6	5			4				10	
																			21	
					3						1								3	
					8							10	3		2			1	1	
25	11	13			399	10		4	4		59	36	5	14	21	23	6	3	23	
																				3
						23	2	1			3									
						16	6			1	44	12		1	1					
						70	14				15	37			5					6
						4	2								1					1
						18	3	4	5	2	32				1				2	
						9	7			1	3				1	13		1	1	
						4	2												2	
						1														
						10														
						4	2	1			8									4
3	4	5	1		221	3					44	21	32	24	4	11	3	3	19	
						4	5													
						1	1													
						13	31				31	68	7	1	8			1	14	
						1														
						53	6			1	1	5	5	14		2	1		44	
7	3	5	1		114	4		1			22	12	1	3	20	22	2	13	57	
						1	3													
						8	1													
						5					1									
						2														
						2														
						20	1	2		5	1						1	1	1	
						42														
27	2	24		2	285	6	3	2	10	95					2	3		93	16	
						242	2		7	102		9			8	8	2	198	162	
2	6	11			262	3	9	1	10	49					3	7	42	24	51	

## APPENDIX 1. Continued.

Bird species <sup>1</sup>	Number of invertebrate items (size in mm)													
	Gas- tro- poda (0-10)	Deca- poda; crabs (0-10)	Iso- poda (5-10)	Scor- pion- oidea (5-30)	Ara- neae (0-5)	Ara- neae (5-15)	Ixodi- dae (0-5)	Diplo- poda (>20)	Chilo- poda (10- 25)	Odo- nata (10- 25)	Or- thop- tera (0-5)	Or- thop- tera (5-25)	Isop- tera (5-15)	Pso- cop- tera (0-5)
<i>Thraupis glaucocolpa</i>														
<i>Tachyfonus rufus</i>		1			3									
<i>Coryphospingus pileatus</i>		3											4	
<i>Saltator albicollis</i>														
<i>Cardinalis phoeniceus</i>								1						
<i>Volatina jacarina</i>														
<i>Tiaris bicolor</i>					2		1						10	
<i>Molothrus bonariensis</i>					5									
<i>Icterus nigrogularis</i>		1			1			2						

<sup>1</sup> Nomenclature following AOU (1983) and Phelps and Meyer de Schauensee (1979).



APPENDIX 2. Number of emetic samples containing each identified plant<sup>1</sup> and percentage of samples with fleshy fruits, seeds, and pollen for each bird species.

Bird species	Number of emetic samples												
	<i>Acanthocereus tetragonus</i>	<i>Bromelia pinaguin</i>	<i>Bursera kars-teniana</i>	<i>Caparis odoratisima</i>	<i>Cap-sicum sp.</i>	<i>Cas-earia syl-ves-tris</i>	<i>Cas-tela erecta</i>	<i>Cordia curas-savica</i>	<i>Croton rham-nifolius</i>	<i>Doy-erea emeto-catar-tica</i>	<i>Ery-throx-ylum cum-nense</i>	<i>Ery-throx-ylum sp.</i>	<i>Gossy-pium hir-sutum</i>
<i>Glaucis hirsuta</i>													
<i>Chlorostilbon mellisugus</i>													
<i>Thalurania furcata</i>													
<i>Leucippus fallax</i>								1					
<i>Amazilia fimbriata</i>													
<i>Amazilia tobaci</i>													
<i>Hypnelus ruficollis</i>											1		
<i>Melanerpes rubricapillus</i>											1		
<i>Xiphorhynchus picus</i>													
<i>Lepidocolaptes souleyetii</i>		1											
<i>Thamnophilus doliatus</i>													
<i>Formicivora grisea</i>													
<i>Camptostoma obsoletum</i>													
<i>Phaeomyias murina</i>			2	9		1		2		20	1	40	2
<i>Sublegatus modestus</i>			1	1	1						3		
<i>Myiopagis viridicata</i>								1					
<i>Elaenia parvirostris</i>								1		2	2		
<i>Elaenia strepera</i>													
<i>Euscarthmus meloryphus</i>													
<i>Atalotriccus pilaris</i>													
<i>Idioptilon margaritaceiventris</i>											1		
<i>Tolmomyias flaviventris</i>													
<i>Cnemotriccus fuscatus</i>											1		
<i>Contopus cinereus</i>													
<i>Myiarchus tyrannulus</i>			1	4	1					3	3		
<i>Pitangus sulphuratus</i>				1									
<i>Myiozetetes similis</i>													
<i>Chiroxiphia lanceolata</i>													
<i>Polioptila plumbea</i>													
<i>Mimus gilvus</i>	3	10		15			2			11	12	1	
<i>Vireo olivaceus</i>			2	4							2		
<i>Hylophilus flavipes</i>			8	15						14	4	16	
<i>Protonotaria citrea</i>													
<i>Coereba flaveola</i>	1										1		
<i>Conirostrum bicolor</i>													
<i>Thraupis glaucocolpa</i>		2		8							4		
<i>Tachyfonus rufus</i>		21									16		1
<i>Coryphospingus pileatus</i>													
<i>Saltator albicollis</i>											1		
<i>Cardinalis phoeniceus</i>		5	5						3	1		1	
<i>Volatina jacarina</i>													
<i>Sporophila lineola</i>													
<i>Tiaris bicolor</i>				1									
<i>Molothrus bonariensis</i>													
<i>Icterus nigrogularis</i>		1											

<sup>1</sup> Nomenclature following Hoyos (1985) except for cactaceae as per Trujillo and Ponce (1980).<sup>2</sup> *Opuntia caracasana* and *Opuntia elator*.<sup>3</sup> Refers either to dry fruits or to fleshy fruits whose seeds were pounded in samples.

APPENDIX 2. Extended.

											Number of emetic samples					
<i>Gua-</i>	<i>Jac-</i>	<i>Lyci-</i>	<i>Mal-</i>	<i>Melo-</i>	<i>Pilo-</i>	<i>Pithe-</i>	<i>Ruella</i>	<i>Sola-</i>	<i>Sola-</i>	<i>Sub-</i>	<i>Tour-</i>	<i>Tri-</i>	<i>Zan-</i>	% of	% of	% of
<i>pira</i>	<i>quinia</i>	<i>um</i>	<i>pighia</i>	<i>cactus</i>	<i>soce-</i>	<i>cello-</i>	<i>tuberosa</i>	<i>num</i>	<i>num</i>	<i>pilo-</i>	<i>nefor-</i>	<i>chilla</i>	<i>thoxy-</i>	samples	samples	samples
<i>micro-</i>	<i>revo-</i>	<i>nod-</i>	<i>glabra</i>	<i>caesius</i>	<i>reus</i>	<i>bium</i>		<i>num</i>	<i>num</i>	<i>ceruus</i>	<i>tia</i>	<i>trifol-</i>	<i>lon</i>	with	with	with
<i>fila</i>	<i>luta</i>	<i>sum</i>			<i>Opun-</i>	<i>morit-</i>	<i>oblong-</i>	<i>num</i>	<i>num</i>	<i>sp.</i>	<i>scandus</i>	<i>liata</i>	<i>ptero-</i>	fleshy	fleshy	fleshy
					<i>tia</i> <sup>2</sup>	<i>zianus</i>	<i>um</i>	<i>num</i>	<i>num</i>				<i>rota</i>	fruits	seeds <sup>3</sup>	pollen
														0	0	100
														0	0	50
														0	0	50
		1												2	2	55
														0	0	100
														0	4	33
														13	0	0
					1	2	1				1		1	67	0	0
														0	4	0
						2								6	0	0
														11	0	0
		1									1			2	1	0
		1												0	0	0
7		7		1		2		1	3		29	9	5	81	1	0
1		9				1			1		9		3	19	3	0
											1			17	0	0
1		6							1		1			93	0	0
														100	0	0
											3			60	0	0
			2	1		1			2		6		1	10	4	0
											1			17	0	0
														8	8	0
		1											1	12	4	0
		1												100	0	0
1	1	2					2				3	1		51	3	0
														50	50	0
														100	0	0
1														100	0	0
														3	4	0
2	9	24	1	5		7	1		1		7	10	4	91	1	0
2											2			27	2	0
3		2		1					3	1	10	17	5	83	4	0
														3	0	0
		2		1		24					7	19		12	3	64
														1	0	0
	12	1				3			1				9	2	100	0
	2	1		7	1	2			4		1		9	80	6	0
		2		4		5				2		1		5	59	0
														1	100	0
	1	13		10		3		1	3	1			2	48	84	0
														0	50	0
														0	100	0
					22	16			1		2			8	95	0
														75	50	0
						1	1							22	0	0