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DIETARY RELATIONSHIPS OF MIGRANT AND RESIDENT BIRDS FROM A HUMID FOREST IN CENTRAL PANAMA

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ABSTRACT.—This study reports on food selection by Nearctic migrants, especially thrushes (*Catharus*), wood-warblers (*Oporornis, Seiurus, Wilsonia*), and tyrant flycatchers (*Empidonax*) in a humid forest of central Panama. We attempt to determine how these migrants integrate into the resident bird community based on local food abundance and diet comparison between resident and migrant species. At our study site, migrants are most numerous during migration periods, especially in October when abundance of arthropods is low and fruits are plentiful. Migrants feed equally on fruits during both migrations, but overall depend more on an invertebrate diet. Actually, migrants feed extensively on a few invertebrate taxa that are mostly of two types: (1) small hard-bodied foliage-dwelling insects such as beetles and ants, which are of low nutritional value; and (2) invertebrates well known for producing distasteful or toxic chemicals, such as nonflying termites, millipedes, and centipedes. In contrast, the resident species feed more extensively on invertebrates of higher nutritional value (spiders, insect pupae, alate ants) and on large prey that are plentiful at tropical latitudes (orthopterans, lizards). Dietary relationships among species show that diet of migrants overlap little with that of resident species, even those with which they share a similar foraging substrate. However, unlike residents, migrants belonging to the same foraging guild have a highly similar diet. These results suggest that past competitive interactions between migrants and residents were more important than the ones among migratory species in determining food selection by migrants. Whether the resulting high potential for competition among migrants is related to the short stay of most species at our study site or is a characteristic of several migrant populations at tropical latitudes needs further investigation. *Received 8 June 1995, accepted 6 September 1995.*

THE FEEDING ECOLOGY of Nearctic migrants in the Neotropics has received considerable attention over the last few decades (e.g. Keast and Morton 1980, Hagan and Johnston 1992, Martin and Finch 1995). Several lines of evidence suggest that migrants either complement resident species by filling unused niches (Hespenheide 1980, Rappole and Warner 1980) or depend on temporally superabundant resources that are underexploited by resident birds (Willis 1966, DesGranges and Grant 1980, Lefebvre et al. 1994). Considering the wide diversity of Neotropical habitats used by migrants and the differing spatial and temporal use they make of these habitats, ecological roles of migrants within tropical communities are certainly diverse, varying according to species, habitat, and geographic range, as well as over the course of the wintering period.

Although food selection by a species is a major aspect of its ecological niche within the bird community, few studies (Morton 1980, Lefebvre et al. 1992a) have investigated the diet of migrants per se. Information on migrants' diet is mostly limited to observation of birds at flowers (DesGranges and Grant 1980), fruiting trees (Leck 1972, Hilty 1980, Greenberg 1981, Scott and Martin 1984), or army-ant swarms (Willis 1966, 1980). Most studies on migrants' feeding habits have focused on foraging methods and microhabitats used. Although these factors will influence the range of prey available to a bird species, it provides no information on how opportunistic or selective are birds in their prey choice. Direct examination of diet is a useful tool to evaluate feeding interactions among species because, in addition to providing indirect information on the foraging substrate and method used, it gives further insight on the diversity of prey taken, as well as their nutritional value. There are no previous studies on bird-community ecology comparing diets of resident and migrant species exploiting the same Neotropical habitat.

We report on food selection by migrants, especially thrushes (*Catharus*), wood-warblers (*Oporornis, Seiurus, Wilsonia*), and tyrant flycatchers (*Empidonax*) that exploit a humid forest in central Panama over the wintering period, but mostly during migration. We attempt to determine how migrants integrate into the resident community based on local food abundance and diet comparison between resident and migrant species. In particular, we answer the following questions: Is migrant abundance related to the exploitation of specific food types that are particularly abundant during their presence at our study site? Do resident and migrant species differ in the use they make of the different food taxa available? How similar are the diets of migrant and resident species using the same foraging substrate? Is diet segregation among migrants from the same foraging guild comparable to that of their resident counterparts?

STUDY AREA AND METHODS

Our study was conducted in a second-growth humid forest near Gamboa in central Panama (9°10′N, 79°7′W). The study site was in Soberanía National Park, covering an area of 3.2 ha along Pipeline Road between the Frijoles and Frijolito rivers. Mist netting was conducted for 7 h beginning at sunrise during three consecutive days twice monthly from September 1993 through November 1994. Thirty-six nets (3 m × 10 m, 32-mm mesh) were placed every 25 m along eight transects 35 m distant. Each bird caught was banded and forced to regurgitate, following the method of Poulin and Lefebvre (1995). However, only the emetic samples collected between September and May (i.e. when migrants were present at our study site) have been used to determine the diet of both migrant and resident species in this paper.

Food items from the regurgitations were preserved in 70% ethanol and identified to order (invertebrate) or species (fruit, pollen). Invertebrate prey within each order were grouped into 5-mm-interval size classes. Subadult forms of insects were classed as eggs, pupae, or larvae without taxonomic distinction. Overall, 27 animal taxa, 65 fruit species, and 89 pollen species were identified in diet samples. To calculate diet similarity among bird species, animal prey taxa were clumped into seven ecological categories: nonflying air/foliage arthropods (Araneae); flying air/foliage arthropods (Hymenoptera [wasps, alate ants], Diptera, Homoptera, Heteroptera, Orthoptera, Odonata, Lepidoptera, Neuroptera, Psocoptera); hard-bodied foliage arthropods (Coleoptera, Hymenoptera [ants]); soft-bodied foliage arthropods (Dermoptera, Isoptera [termites]); inactive foliage arthropods (insect egg, nymph, pupae, larvae); ground-dwelling invertebrates (Gastropoda [snails], Isopoda, Diplopoda [millipedes], Chilopoda [centipedes], Crustacea [crabs], Scorpionidae, Pseudoscorpionidae); and vertebrates (frogs, lizards). The sizes of animal prey were evaluated through the numbers of items belonging to each of these three categories: (1) 0–5 mm; (2) >5–15 mm; and (3) >15 mm. Similarly, the 65 fruit species found in the regurgitations were classified into five fruit types: small seed fruits; midsize seed fruits; large seed fruits; dry fruits; and large fruits. Number of fruits taken was extrapolated from the number of seeds counted in the regurgitation. Nectar intake was estimated by the number of species of pollen found in each sample.

Relative abundance of arthropods was estimated twice monthly from sweep-net samples. The first 2 m of vegetation were swept with a standard insect net during 20 min in late morning. Arthropods were identified, sized, and counted as for the regurgitation samples. All taxa taken by the birds were sampled with sweep net. Furthermore, the proportion of arthropods from each taxa in sweep-net samples was positively correlated with that found in regurgitations ($r_s = 0.720$, df = 23, $P < 0.001$), suggesting that sweep-net samples provide a reasonable estimate of food available to birds. Abundance of fruit was estimated twice monthly using 60 litter traps (0.5 m × 0.5 m) placed 0.25 m above ground every 10 m along the net transects. This method samples fruits (seeds) falling from trees and shrubs, as well as those defecated or regurgitated by animals. Only fruit species identified in regurgitation samples were considered to determine fruit abundance over time. To reduce bias associated with patchy distribution of fruits, their abundance was estimated by counting the number of traps in which a fruit species was found, instead of the total number of fruits sampled from that species.

Diet preference based on animal prey taxa, animal prey size, and types of fruit taken was compared between residents and migrants as a whole using *G*-tests. At the species level, diet similarity (overlap) was calculated using Pianka's formula (*SIMI*; Pianka 1973, Rotenberry 1980):

$$SIMI = \sum_{i=1}^{n} (x_i y_i) \Bigg/ \left(\sum_{i=1}^{n} x_i^2 \sum_{i=1}^{n} y_i^2 \right)^{0.5}, \qquad (1)$$

where x_i is the proportion of a specific food category in the diet of one bird species, y_i is the proportion of a specific food category in the diet of a second bird species, i is the food category, and n is the number of food categories in the diet of the two bird species. This index was calculated based on the proportion of food items among 16 categories including the seven ecological categories of animal prey, the three prey-size classes, the five fruit types, and nectar intake. Only the bird species represented by five emetic samples or more totalling at least 20 identified food items were considered in the analysis. With the exception of the Canada Warbler (*Wilsonia canadensis*, $n = 5$), all species were represented by 10 diet samples or more, which should provide an adequate sampling effort for diet estimation (Sherry 1984). The similarity matrix was submitted to a principal coordinates analysis (Legendre and Legendre 1983) to reveal diet relationships among 31 resident and 7 migrant bird species. To facilitate interpretation of dietary relationships among birds, each species was assigned to a broad foraging guild based on the main food type and feeding substrate they use (Willis 1966, Ridgely and Gwynne 1989, Stiles and Skutch 1989). Foraging guilds were nectarivores, frugivores, and insectivores, the latter being divided into aerial foragers, foliage gleaners, bark foragers, and ground foragers.

RESULTS

Migrant abundance.—We caught 1,484 residents and 143 migrants between September and May. Nearctic migrants were captured throughout the wintering period, but mostly during fall migration, when they represented up to 25% of the mist-netted birds. Thrushes (*Catharus ustulatus, C. minimus, C. fuscescens*) were the most abundant migrants with a major peak in October and a second one in April (Fig. 1). Two Wood Thrushes (*Hylocichla mustelina*) were also captured in both February and November. Wood-warblers (*Oporornis formosus, Seiurus noveboracensis, S. aurocapillus, Wilsonia canadensis, Protonotaria citrea, Mniotilta varia, Dendroica striata,* and *D. pensylvanica*) were caught throughout the winter, but mostly during migration (Fig. 1). Finally, two flycatcher species were sampled—*Contopus virens* during fall migration, and *Empidonax virescens* throughout the wet season (Fig. 1).

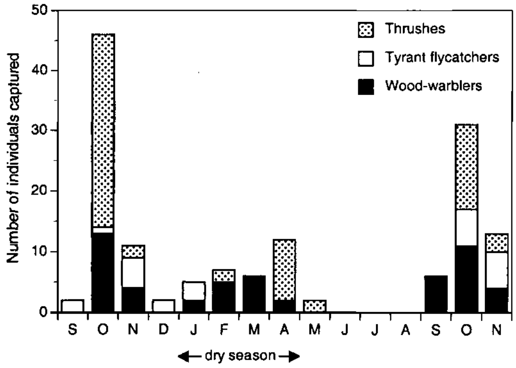

Fig. 1. Temporal variation in migrant abundance.

Food abundance.—The study site has an average annual precipitation of 2,133 mm and is characterized by a severe dry season from January through April. During the wet season, mean monthly rainfall is constant from May through September, peaks in October, and reaches a low in December. Arthropods sampled with sweep net showed a maximal abundance at the beginning of the wet season (May–June) and minimal numbers in October when rainfall was highest (Fig. 2). This pattern was not related to a few abundant taxa, since most invertebrate categories followed that same trend (Fig. 2). Fruit abundance pattern differed among the various fruit types (Fig. 2). Berrylike fruits with numerous tiny seeds, such as *Miconia*, showed a major peak in the late wet season (November) and a second one in the late dry season (April). Fruits bearing from one to five medium-sized seeds (e.g. *Psychotria*) peaked a month earlier. Fruits bearing large seeds (>8 mm long) were sampled mostly during the dry season (January through April). Dry fruits were abundant in June and September. Finally, large fruits from which only a portion could be taken by the birds were more common during the

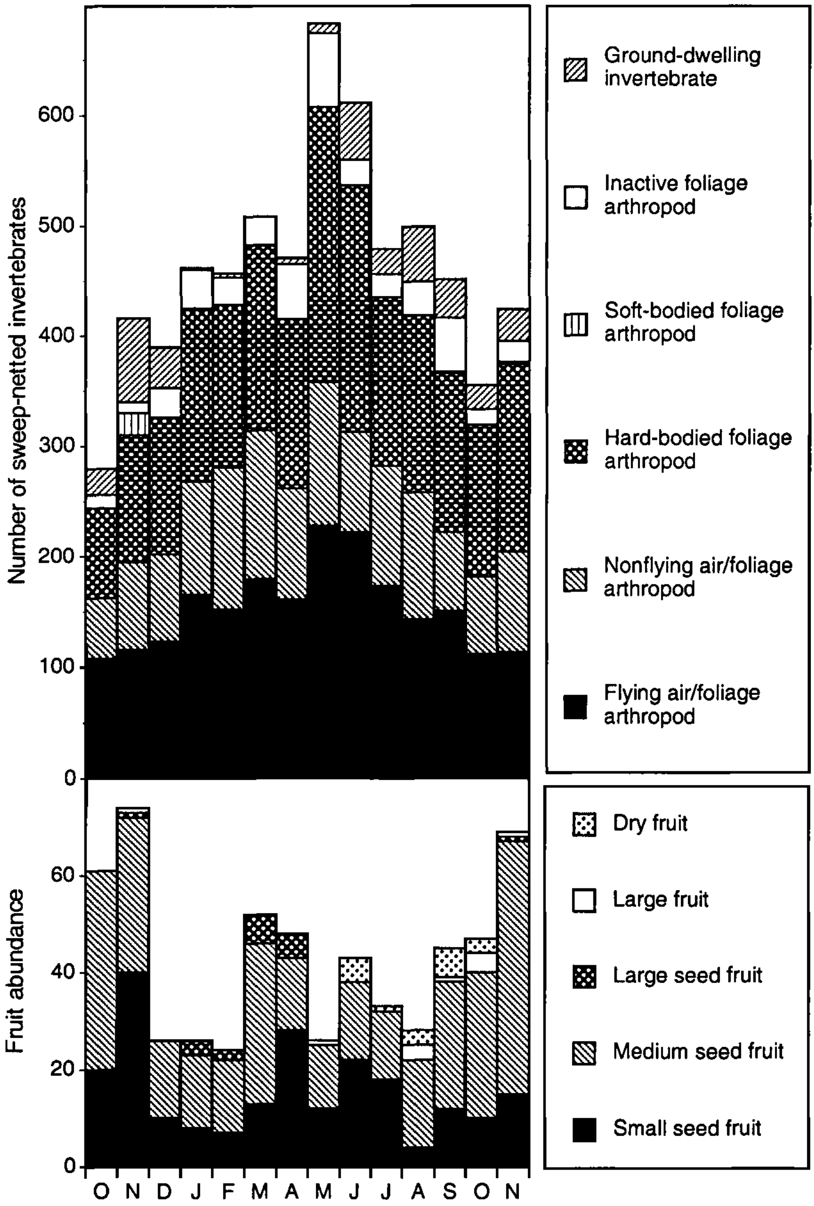

FIG. 2. Temporal variation (October 1993 through November 1994) in abundance of invertebrates sampled by sweep net and of fruits collected in fruitfall traps, with distinction of ecological prey category (see Methods for taxonomic affinity) and fruit type.

second part of the wet season (August–October).

Bird diet.—Migrant and resident species differed in the use they made of the different invertebrate taxa available (Table 1). Overall, migrants fed more frequently on nonflying ants, beetles, and insect larvae than did resident species, although these insect prey were common in the diet of the resident species as well. Gastropods (snails) represented a higher proportion of the diet of migrants compared to residents, while *Catharus*, *Seiurus*, and *Oporornis* regularly fed on them. Finally, migrants fed significantly more on nonflying termites, centi-

TABLE 1. Diet comparison between migrant and resident species. Significant differences (G-tests) shown by asterisks (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$).

	No. items/100 samples			
	Migrants (n = 143)	Statistical difference	Residents (n = 1,484)	No. items taken
Prey taxa				
Hymenoptera (ants)	167.8	***	21.8	563
Coleoptera (beetles)	130.8	***	46.2	873
Isoptera (termites)	80.4	***	0.1	116
Diplopoda (millipedes)	44.1	***	2.6	101
Insect larvae	36.4	*	25.7	433
Gastropoda (snails)	15.4	***	0.4	28
Chilopoda (centipedes)	2.1	**	0.1	5
Insect eggs	33.6		35.0	568
Hymenoptera (wasps)	17.5		11.4	194
Heteroptera	9.8		9.7	158
Diptera	2.8		3.6	58
Isopoda	0.7		0.9	15
Odonata	0.7		0.9	15
Lepidoptera (adults)	0.0		0.5	8
Frogs	0.0		1.3	19
Hymenoptera (alate ants)	0.0	*	2.0	29
Insect pupae	0.0	**	2.8	42
Lizards	1.4	*	5.1	77
Homoptera	2.1	*	6.1	94
Orthoptera	7.7	**	16.3	253
Araneae (spiders)	19.6	***	68.3	1,042
Prey size				
0–5 mm	423.1	***	160.5	2,987
>5–10 mm	109.1	***	52.2	930
>10–15 mm	23.1		21.8	356
>15–20 mm	4.9		7.1	112
>20–25 mm	3.5		7.0	109
>25 mm	3.5	***	13.1	199
Fruit type				
Small seed fruits	25.9	***	12.3	219
Medium seed fruits	65.0	***	7.7	208
Dry fruits	4.2		3.2	54
Large seed fruits	2.8		2.3	38
Large fruits	0.7		1.9	29

TABLE 2. Fruit intake by migrant species.

Bird species	No. samples	No. fruits taken	No. fruit species	Percent of samples with fruits
Catharus ustulatus (fall)	25	54	17	80
C. ustulatus (spring)	11	27	6	73
C. minimus	15	14	6	47
C. fuscescens	10	27	12	60
Hylocichla mustelina	4	4	1	25
Other species	78	9	5	9

pedes, and millipedes than the residents. Millipedes were not taken only by species that forage typically on the ground such as thrushes, but also by tyrant flycatchers (*Contopus*, *Empidonax*), and wood-warblers (*Oporornis*). These seven taxa accounted for 83% (682/822 items) of the invertebrate diet of all migrant species.

In contrast, residents fed significantly more on spiders, orthopterans, homopterans, lizards, insect pupae and alate ants than migrants (Table 1). These taxa accounted only for 38% (1,493/3,888 items) of their animal diet.

Some differences also were observed in prey size (Table 1). Migrants fed more extensively on small invertebrates (74% of all items taken), whereas prey longer than 15 mm consistently were more important in the diet of the resident species.

Finally, migrants showed a clear preference for berrylike fruits with seeds of small to medium size, and seemed to avoid feeding on large fruits. The thrushes clearly were more frugivorous than any other migrant species (Table 2), but *Empidonax virescens*, *Dendroica pensylvanica*, *D. striata*, and *Seiurus aurocapillus* also fed on fruits. *Psychotria* (61 fruits taken from nine species), *Miconia* (25 fruits from two species), *Palicourea* (19 fruits), and *Conostegia* (9 fruits) represented 84% of all fruits taken by migrants. The occurrence of these fruit species in the emetic samples was significantly higher for migrants than residents ($G = 68.8$, df = 1, $P < 0.001$). Nevertheless, animal food was more important than fruits in the diet of any migrant species, in terms of both number of items taken and proportion of samples in which each food type appeared.

Dietary relationships.—Dietary relationships among the 38 bird species submitted to the principal coordinates analysis are summarized in Figure 3. The Euclidean representation of the first two axes of the analysis is adequate based on the criteria suggested by Cailliez and Pagès (1976). The clumping of the various food taxa into a few categories allowed segregation of diets, since the bird species are almost uniformly distributed in the ordination diagram.

Among resident species, only nectarivores and frugivores showed a relatively high diet simi-

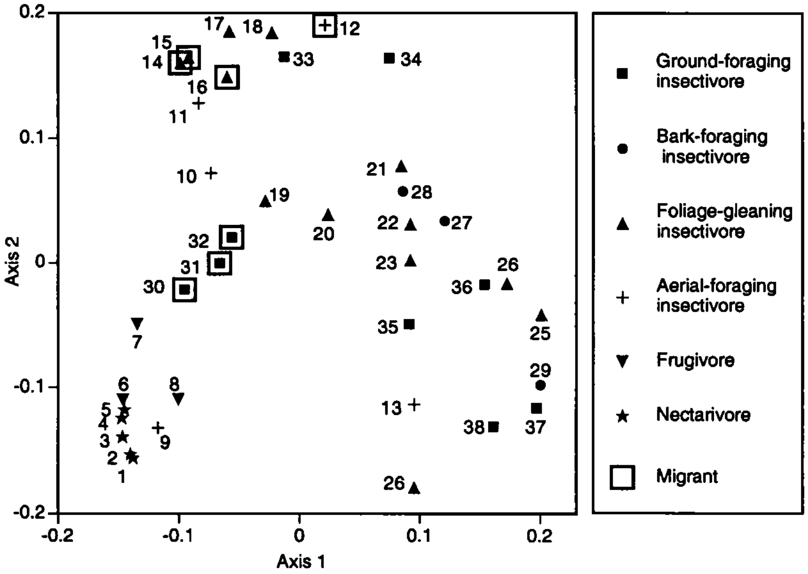

Fig. 3. Ordination of bird species based on diet similarity using principal coordinates analysis. Species corresponding to each number listed in Table 3.

larity among them, each one of these guilds being confined to a small portion of the diagram. These birds feed primarily on nectar (hummingbirds) or fruits (manakins), and their arthropod diet is limited to a few prey taxa (Table 3). The high numbers of nectarivores and frugivores sampled, as well as their low recapture rates, are consistent with a high diet overlap, since the birds' movements allow them to feed on locally abundant flowers and fruits (Loiselle and Blake 1992).

There is no tendency for the resident insectivores belonging to a same foraging group to be clumped together. The low diet overlap among these residents is related to the variety of arthropods taken from different prey categories. This was especially obvious for aerial foragers that are widely distributed in the ordination diagram (Fig. 3): *Mionectes oleagineus* fed almost exclusively on spiders and small fruits; *Attila spadiceus* fed extensively on lizards in addition to flying insects; finally, *Terenotriccus erythrurus* and *Oncostoma olivaceum* fed mostly on the wing, but supplemented their diet with nonflying and subadult insects (Table 3). The other three groups of resident insectivores are intermixed and occupy the portion of the diagram on the right. There is little grouping of these species by their foraging guild and, frequently, the species most similar in diet do not use the same foraging substrate. Resident gleaning insectivores supplemented their diet with either fruits, seeds or flying insects, and also differed by the use they make of vertebrates, subadult insects and spiders (Table 3). Among bark foragers, *Xiphorhynchus* differed from the other two species by its high intake of insect larvae and low intake of spiders and ants (Table 3). Finally, resident ground foragers differed mostly in the use they made of spiders, beetles, and ants, as well as in the size of prey taken (Table 3).

In contrast, the diets of migrant species belonging to the same foraging guild were highly similar, as shown by the tight grouping of migrant foliage gleaners and migrant ground foragers in the ordination diagram (Fig. 3). Differences in diet overlap between migrants and residents are obvious when comparing the mean diet similarity values between species from a same foraging group (Table 4). Even the resident bark foragers—represented by only three species and two genera—overlapped less in their diet than migrants from any foraging guild (Table 4). Diet overlap among migrants was rather similar to the values obtained for nectarivorous and frugivorous resident species (Table 4). However, in contrast to nectarivores and frugivores, *Catharus* thrushes fed on a large variety of food types (Table 3). Their high diet simi-

TABLE 3. Diet of most-abundant resident and migrant species. Number of items taken indicated for each food category: (A) flying air/foliage arthropods (orthopterans, bugs, wasps, others); (B) nonflying air/foliage arthropods (spiders); (C) hard-bodied foliage arthropods (beetles, ants); (D) soft-bodied foliage arthropods (termites); (E) inactive foliage arthropods (insect larvae, eggs and pupae); (F) ground-dwelling arthropods (snails, millipedes, others); (G) vertebrates (frogs and lizards); and plant food (fruit, pollen).

	A				B	C		D	E		F			G	Prey size		Plant food	
Bird species	ort	bug	was	oth	spi	bee	ant	ter	lar	e/p	sna	mil	oth	ver	≤5 mm	>5 mm	fru	pol
Nectarivores																		
1 *Phaethornis longuemareus*					9										9			42
2 *P. superciliosus*			3	1	99	1	2		2						100	8		2 242
3 *Thalurania colombica*			3	1	16				1						21			7
4 *Amazilia amabilis*	1		44	23	133	4	1		5						207	4		74
5 *Damophila julie*	2		61	27	137	4	1		7						237	2		69
Frugivores																		
6 *Manacus vitellinus*							1								1		36	
7 *Pipra coronata*	3	2	3	4	19	26	1		6				2		55	11	124	
8 *P. mentalis*			2	1	33	8	2		17	5					48	20	352	
Aerial-forager insectivores																		
9 *Mionectes oleagineus*				1	221	2	2		1						194	33	111	3
10 *Terenotriccus erythrurus*	6	1	1	15	3	18				18		1			52	11		
11 *Oncostoma olivaceum*	7	4	3	27	13	94	7		7	58					182	38	3	
12 *Empidonax virescens*[a]		5	7	4	6	41	30		2			1	1		53	44	3	
13 *Attila spadiceus*	1		1	3		2	2							10	5	14	3	
Foliage-gleaner insectivores																		
14 *Seiurus noveboracensis*[a,b]		1			4	25	62			8	2				100	2		
15 *Oporornis formosus*[a,b]	6	2	5	2	12	47	108		4	22	9	4		1	196	27		
16 *Wilsonia canadensis*[a]	1	4	6			16				2					23	6		
17 *Xenops minutus*	8		1	2	3	8	42		1	3					52	16		
18 *Hylophylax naevioides*	4	3	3	9	7	104	9		6	29		4	1	14	124	69		
19 *Myrmotherula axillaris*	4			1	15	12			2	2					23	13		
20 *Cyanocompsa cyanoides*					4	11			1						8	8	36	
21 *Eucometis penicillata*	5	2	2	1	5	10	5		2	1				1	14	20	13	
22 *Myrmotherula fulviventris*	35	4	1	2	73	43	11		2	53			2	4	98	132		
23 *Tachyphonus luctuosus*	7		1	4	2	9			3	1					10	17	19	
24 *Thamnophilus punctatus*	38	48		17	19	49	9		45	109	2			9	96	250		
25 *Myrmeciza exsul*	5	2		1	4	6	2		8	8		2		6	9	34		
26 *Schiffornis turdinus*	1					1			44						1	45	29	
Bark-forager insectivores																		
27 *Dendrocincla homochroa*	5	1		2	12	10	1			2				2	12	22		
28 *D. fuliginosa*	18	15	11	9	35	42	13		1	74		1	4	16	109	130		
29 *Xiphorhynchus guttatus*	7	10		2	7	7			25	27				2	4	83		
Ground-forager insectivores																		
30 *Catharus fuscescens*[a]		1		1		8	2	15	1		2	11	2		28	12	27	
31 *C. ustulatus*[a]				2		15	15	29	20	1	3	15	2		62	38	81	
32 *C. minimus*[a]	1					23	9	71	18		4	23	1	1	94	49	14	
33 *Sclerurus guatemalensis*	4				15	54	1		6	3		8	4	4	58	38		
34 *Formicarius analis*	8	3		1	4	38	50		9	11		11	5	8	60	88	1	
35 *Cyphorhinus phaeocephalus*	3	1			12	3			1			3	2	1	10	16		
36 *Gymnopithys leucaspis*	28	5		5	45	22	8		9	9		1	3	8	43	99		1
37 *Phaenostictus mcleannani*	5			1	5	1						1		2	1	14		
38 *Baryphthengus martii*	2	2				5			3	1	1	3		1	1	17	6	
Total	215	116	158	169	972	769	396	115	259	447	23	89	29	90	2,400	1,430	860	438

[a] Migrant species.

[b] Also ground foragers.

TABLE 4. Comparison of diet-similarity values between each foraging guild with distinction of migrant and resident species.

Foraging guild	Diet-similarity value Mean	Minimum
Resident species		
Nectarivores	0.9175	0.8366
Frugivores	0.9525	0.9457
Aerial-forager insectivores	0.6013	0.2831
Foliage-gleaner insectivores	0.6620	0.0253
Bark-forager insectivores	0.7870	0.7107
Ground-forager insectivores	0.6239	0.2851
Migrant species		
Foliage-gleaner insectivores	0.9518	0.9172
Ground-forager insectivores	0.9263	0.9044

larity is related to the fact that they fed on the same arthropod taxa and fruit types in similar proportion. Thrushes also have a ratio of small versus large prey taken of 2:1, which is unusual among the bird community (Table 3). The high diet overlap among wood-warblers is mostly related to their similar intake of hard-bodied and inactive foliage arthropods, and flying and nonflying air/foliage arthropods, as well as to their avoidance of fruits and preference for small animal prey (Table 3).

Diets of migrants, however, showed little overlap with that of resident species, even those with which they share a similar foraging mode (Fig. 3). Migrant thrushes differed from the resident ground foragers by their high intake of termites, millipedes, and fruits, as well as by their low intake of spiders and vertebrates (Table 3). Wood-warblers, especially *Oporornis* and *Seiurus*, differed from most resident gleaners by their intake of ants and gastropods, whereas *Wilsonia* fed more importantly on flying insects (Table 3). Finally, *Empidonax*, the only migrant aerial forager for which enough data were collected, differed from its resident counterparts by the extensive use it made of both beetles and ants (Table 3).

DISCUSSION

Because fall migration coincides with the tropical wet season, it is often assumed that migrants arrive at their wintering ground during a period of high arthropod availability (Russell 1980, Schwartz 1980). However, several studies show that arthropods peak primarily at the onset of the rainy season and decrease afterward (e.g. Buskirk and Buskirk 1976, Willis 1976, Smythe 1982, Levings and Windsor 1985, Poulin et al. 1992). At our study site, foliage-dwelling arthropods reach their lowest numbers in October when migrant abundance is highest.

Although there are some reports of fruit intake by migrants during fall migration (Leck 1972), frugivory generally is considered to be more important during the dry season and spring migration (Morton 1971, Greenberg 1981, Scott and Martin 1984). Our results show that migrants feed equally on fruits during both migrations, although fruits as a whole are most abundant during the fall.

Most migrant species, however, depend mainly on an invertebrate diet at our study site. They do not feed opportunistically on superabundant arthropods, but rather specialize on a few invertebrate taxa which are basically of two types. The first type are nonflying termites, millipedes, and centipedes, invertebrates rarely taken by the resident birds and well known for producing distasteful or toxic chemicals (Cloudsley-Thompson 1968, Moore 1969, Hopkin and Read 1992). The second group are small hard-bodied insects, such as beetles and nonflying ants, which are commonly taken by the resident species as well, although to a lesser extent. Because these insects are found on every substrate and are relatively easy to prey upon, they represent an important part of the arthropod diet of several species in tropical bird communities (Lefebvre et al. 1992b, Poulin et al. 1994, this paper). However, their low nutritive value (low fat content, high proportion of cuticle not digested by most birds; Bell 1990) and the fact that they are taken frequently but always in small amounts and, more importantly, when overall abundance of arthropods is low (Poulin unpubl. data), suggest that these prey are just a "better-than-nothing" food to the birds. The number of beetles and ants in sweep-net samples was especially low in September-October and, consequently, their high intake by migrants cannot be related to local abundance. The reason why migrants forage on these taxa even more frequently than the resident birds could be related to: (1) the migrants' lower foraging success on other prey types; or (2) the birds' recent arrival after migration involving high physiological demands. Temporal intake of beetles and ants by migrants suggests that the second hypothesis is most likely correct. Ants and beetles were taken most frequently in September and March, and least frequently in winter; they were avoided in April–May when the birds are expected to build up fat reserves.

Alternatively, resident birds feed more extensively than migrants on two prey types. The first one involves spiders, insect pupae, and alate ants, which are characterized by a low chitin and/or high fat content (Dalingwater 1987, Bell 1990). The other type refers to orthopterans and lizards, which are large prey particularly abundant and diverse at tropical latitudes.

Overall, the diet of migrants shows little overlap with that of the resident species, even with those using a similar foraging substrate. Moreover, diet relationships among insectivores belonging to the same foraging group were totally different when comparing migrants and residents. While the resident species differed in several aspects of their diet, migrant species from a same foraging group were highly similar in their food choice. A lower diet overlap among resident species is probably related to the fact that these birds coexist year-round, whereas most migrants spend only a few days or weeks at our study sites. Resident species will either feed on a wide variety of animal prey in differing proportions, or specialize on different taxa, which in both cases decrease diet overlap within the bird community. However, migrants of the same foraging guild tend to feed consistently on the same food taxa in similar proportion.

Catharus thrushes were the most abundant migrants at our study site. They commonly feed on fruits during both migrations and this resource is considered as the key factor to their presence in that habitat (Martin 1985). Thrushes were present at our study site when fruits were particularly abundant, suggesting that they are tracking that resource. In several habitats in Costa Rica (Blake and Loiselle 1992) and in Colombia (Hilty 1980), the same species of thrushes are reported to feed on fruits throughout winter. Nonetheless, migrant thrushes feed more extensively on invertebrates than on fruits at our study site. These birds are unique in the sense that they are the almost exclusive consumers of termites, millipedes, and centipedes. As many as 56 millipedes and 115 termites were found in 65 emetic samples from thrushes. Because millipedes occurred in more than 60% of the samples, and termites represented as much as 35% of all invertebrates taken, the distribution of these invertebrates could also be important in habitat selection by migrant thrushes. At our study site, the intake of millipedes by the resident species peaks in June and October, being especially low from December to March. Assuming that the actual number of millipedes taken by the resident bird community is a good estimate of their local availability, the presence of thrushes at our study site would coincide with the period of highest abundance of millipedes. Nonflying termites are presumably available year-round, but are ignored as food source by the resident species.

Winter habitat selection by migrants is probably a compromise between the availability of appropriate food types and the minimization of competitive interactions with resident species. During their short stay in a humid forest of central Panama, migrants feed mostly on small fruits and low-quality invertebrates easy to prey upon. Furthermore, in contrast to resident species, migrants feed little on arthropods that are plentiful at tropical latitudes and/or characterized by a low-chitin or high-fat content. The low quality and diversity of animal prey taken by migrants, as well as the highly overlapping diet among migrant species, suggest that migrants are not well integrated into the tropical bird community. On the other hand, migrants differ from residents in several aspects of their diet, and feed on different food taxa that each represents only a fraction of the diet of several resident species. As a result, there is little diet overlap between migrants and residents using a similar foraging substrate which, alternatively, suggests that each migrant foraging group is well integrated into the Neotropical bird community. Dietary relationships suggest that past competitive interactions between migrants and residents were more important than the ones among migratory species in determining food selection by migrants. Whether the resulting high potential for competition among migrants is related to the short stay of most species at our study site or is a characteristic of several migrant populations in the Neotropics needs further investigation.

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