THE IMPACT OF SOME NORTH AMERICAN MIGRANTS AT FRUITING TREES IN PANAMA

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AMONG the major seasonal phenomena potentially affecting neotropical birds is the winter influx of North American migrants. The subject has been much neglected, except for brief general discussions (Morel and Bourliere, 1962; Miller, 1963) or studies restricted to specialized groups (e.g. Willis, 1966). To gain a new quantified estimation of the effect of migrants I studied their use of local food sources, especially fruiting trees, relative to use by residents.

STUDY AREAS AND METHODS

During March and April 1968, I studied bird use of certain fruits in a highland semi-agricultural area of western Panama (82° W, 8° N), near El Hato (4,000 feet elevation) and Cerro Punta (6,000 feet elevation). Data included the numbers of feeding visits by each species of migrant and resident, and banding population estimates of all species exploiting a particular resource.

From September 1968 through April 1969, I gathered similar data at fruiting and flowering plants in the Panama Canal Zone, particularly at a clearing surrounded by a mature lowland rain forest on Barro Colorado Island (79° W, 9° N). Monthly sightings of all migrants were tabulated and the numbers of common species (including residents) estimated for the study area through color-banding. During the fall wet season I compared the effects of various rain intensities on the foraging of migrants and residents.

Specific names are from Eisenmann (1955).

RESULTS

Barro Colorado Island and the Canal Zone.—Figure 1 shows the occurrence of the commoner migrants at the clearing on Barro Colorado Island. October and early November formed the peak of migrant activity, with the numbers of individuals higher during the fall than in the spring (Table 1). Willis (1966) similarly found migration in the forest of the island to be greatest during the fall and this appears to be true through most of Panama (Galindo and Mendez, 1965; Loftin, pers. comm.). We may then predict any competitive importance of migrants to be greatest in the fall.

Population estimates of wintering migrants in the clearing were similar (Table 2) to those of Moynihan (1962). For two migrants (Summer Tanager and Bay-breasted Warbler) all individuals seemed to be banded. For several residents and two migrants (Red-eyed Vireo and Yellow Warbler) with no bandings, the populations were estimated from the maximum numbers of individuals seen at any one time.

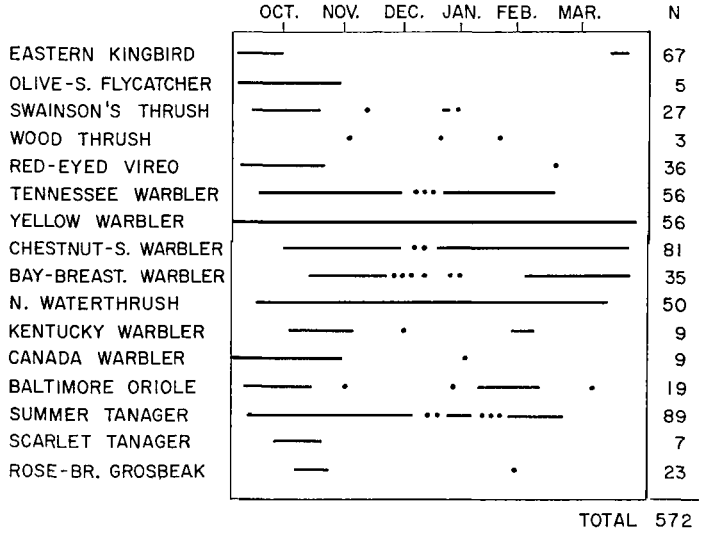

Figure 1. Occurrence of migrants on Barro Colorado Island, at the clearing study area from 21 September 1968 to 13 April 1969. N = total number of sightings (each sighting equals one day per individual bird). Solid lines = periods of regular occurrence, dots = periods of irregular occurrence and individual records.

TABLE 1

COMMON TRANSIENT MIGRANTS DURING FALL AND SPRING IN THE BARRO COLORADO ISLAND CLEARING[1]

Species	Fall (1968) migration		Spring (1969) migration	
	Oct.	Nov.	Feb.	Mar.
Eastern Kingbird	4			
Olive-sided Flycatcher	2	1		
Swainson's Thrush	21	1		
Red-eyed Vireo	23	5		1
Tennessee Warbler	8	14	13	3
Bay-breasted Warbler	8	11	5	5
Kentucky Warbler	3	2	3	
Canada Warbler	5	2		
Baltimore Oriole	5	1	3	1
Summer Tanager	19	24	17	5
Scarlet Tanager	6	1		
Rose-breasted Grosbeak	16	6	1	
Subtotals	120	68	42	15
GRAND TOTALS	188		57	

[1] Data gathered as in Figure 1, with approximately 100 hours in the field for each month. The numbers represent the total numbers of sightings (each sighting equals one day per individual bird).

TABLE 2

POPULATION ESTIMATES FOR COMMON TANAGERS, HONEYCREEPERS, AND WARBLERS AT BARRO COLORADO ISLAND[1]

Moynihan's 1959 estimates[2]	Species	Winter 1968–69[3]	
2	Fulvous-vented Euphonia	8	(6)
10	Plain-colored Tanager	10	(6)
2	Golden-masked Tanager	3	(1)
4	Blue-gray Tanager	3	(2)
4	Palm Tanager	4	(1)
4	Crimson-backed Tanager	1	–
2	*Summer Tanager*	4	(4)
4	Bananaquit	3	(1)
?[4]	Blue Dacnis	8	–
6	Red-legged Honeycreeper	5	–
5	Green Honeycreeper	2	–
?	*Red-eyed Vireo*	3	–
?	*Tennessee Warbler*	3	(2)
2	*Yellow Warbler*	3	–
?	*Chestnut-sided Warbler*	3	(1)
?	*Bay-breasted Warbler*	2	(2)
?	*Northern Waterthrush*	2	(1)

[1] Based on daily observations of the species and notes on the approximate proportions of each species that were banded. North American migrants are in italics.

[2] Moynihan (1962: 15) made these estimates on a subjective basis after several weeks of daily censusing and observation in the clearing, from 26 October to 20 December 1959.

[3] Numbers of color bandings in parentheses.

[4] ? = no data given.

Many of the migrant species were primarily insectivorous. Even the common frugivorous Summer Tanagers spent much time in flycatching for insects. Thus in 100 hours of censusing at a *Cecropia* tree in fall, three resident tanagers (Palm, Blue-gray, and Plain-colored) made 585 fruit-feeding visits, versus 10 from the Summer Tanagers. Similarly at *Oryctanthus* plants the most frequent migrant, the Red-eyed Vireo, made only 49 of the 797 berry-feeding visits recorded during the fall. At all other study plants (more than 50 species) on the island, the migrants contributed even less than at the *Cecropia* and *Oryctanthus*. Hence at this lowland locality it appears that migrants are not likely to compete seriously with the residents for fruit resources, especially during the spring dry season when fruit is superabundant (Leck, 1970, 1972).

Elsewhere in the Canal Zone migrant flycatchers (Fork-tailed Flycatcher, Eastern and Gray Kingbirds) fed with numerous residents at *Ficus* and *Roystonea* trees (Leck, 1969), but the fruit production exceeded exploitation in every month. In fact, migrants often congregated about the unnatural food surpluses of many ornamental trees and shrubs. Even then, migrants only comprised 12 percent (maximum) of all the individuals feeding at specific trees (e.g. ornamental *Ficus* in Balboa).

TABLE 3
EXPLOITATION OF A FIG TREE (*FICUS TURCKHEIMII*) IN PANAMA[1]

Species	A[2]	B[3]	C[4]	D[5]
RESIDENTS				
Sulphur-winged Parakeet	17	17.5	297.5	63
Flame-colored Tanager	13	1.8	23.4	5
Long-tailed Silky Flycatcher	7	3.0	21.0	4
Mountain Robin	10	1.75	17.5	4
Elaenia sp.	12	1.2	14.4	3
Clay-colored Robin	6	2.0	12.0	3
Red-crowned Woodpecker	7	1.25	8.75	2
Yellow-throated Brush-Finch	8	1.0	8.0	2
White-throated Robin	6	1.0	6.0	1
Blue-gray Tanager	3	2.0	6.0	1
Streaked Saltator	5	1.0	5.0	1
Silver-throated Tanager	2	2.0	4.0	1
Acorn Woodpecker	3	1.0	3.0	0.5
Emerald Toucanet	2	1.0	2.0	–
MIGRANTS				
Swainson's Thrush	8	2.7	21.6	5
Baltimore Oriole	6	2.3	13.8	3
Scarlet Tanager	2	3.0	6.0	1
Summer Tanager	2	1.5	3.0	0.5
			472.95	100%

[1] Near El Hato del Volcan, northwest Panama, 16 March–22 April 1968. Observation periods: 16 March, 07:00–10:00; 27 March, 07:00–10:00; 1 April, 10:30–11:30; 4 April, 14:00–18:00; 15 April, 11:00–14:00; and 22 April, 07:00–10:00. For each hour records were maintained of all species feeding on the fruits at the tree.

[2] Number of 1-hour census periods species were recorded (total n = 18).

[3] Average maximum number of individuals hourly.

[4] Product of A and B.

[5] Percentage of total usage.

El Hato and Cerro Punta.—At higher elevations the importance of migrants is reported to be much greater (Willis, 1966), but no such effect was noted at a fig tree at 4,000 feet elevation in western Panama, where migrants contributed only about 10 percent of the total exploitation (Table 3 and Figure 2). In Costa Rica at 4,000 feet elevation, Hespenheide (in litt.) also found migrants rather unimportant at several *Cecropia* trees in March. But at 6,000 feet elevation near Cerro Punta, banding showed Swainson's Thrushes representing 45 percent (n = 110) of all the individuals (n = 245) eating berries at *Leandra* shrubs by April (Leck and Hilty, 1968, and Figure 2). The thrushes were not so plentiful in winter as during this migration month.

In each case (*Ficus*, *Cecropia*, and *Leandra*), no competition was apparent between the residents and migrants as the fruits were superabundant (moderate to heavy fruit drop, few fruit stalks eaten, and many overripe berries, respectively). Thus while limited to the spring, the data again suggest that migrants are not important competitors.

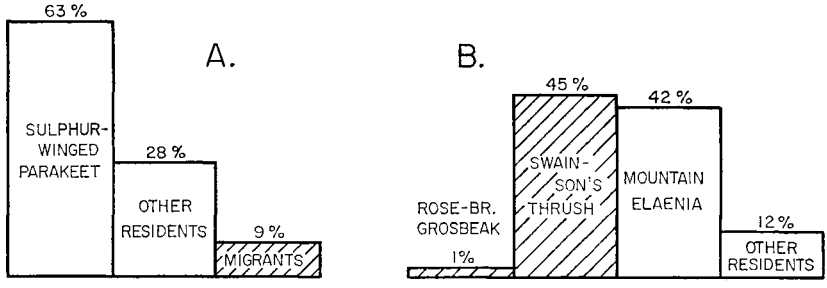

Figure 2. The exploitation of (A) a fig tree (*Ficus turckheimii*) and (B) melastome shrubs (*Leandra subseriata*) in the highlands of western Panama. The large *Ficus* was near El Hato, N. W. Panama; elevation 4,000 feet. The figure is based on the Exploitation Index of Table 3, representing 16 March–22 April 1968. The *Leandra* shrubs were near Cerro Punta, N. W. Panama; elevation 6,000 feet in early April 1968. The figure is based on the number of individuals of each species, as determined through extensive banding.

Foraging during rainy periods.—I studied the foraging behavior of lowland migrants and residents to determine if migrants foraged more than residents in inclement weather. Birds under greater feeding pressures of the wet season would be expected to continue foraging even in unfavorable rainy periods.

Activity of birds at the Barro Colorado Island clearing depended on the intensity of precipitation (Table 4). With a light rain many species continued feeding or foraging, though at a much reduced rate. With moderate rains most of the residents decreased activity further, while the migrants regularly became more active. In the heavy rains both residents and migrants suspended activity and sought shelter. The advantages or requirements involved in the rain feeding must be important for the maintenance energy during such foraging is considerable. Migrants (Eastern Wood Pewee, Chestnut-sided Warbler, Summer Tanager) frequently flicked wings and tail and body-shaked. In moderate rains the wing-flicking rate was as high as 30–35 per minute, and yet birds would get conspicuously wet, contributing further energy losses.

Social behavior of migrants.—Within the migrant passerines of the lowlands only isolated individuals or intraspecific associations were regularly observed. These associations included male-female pair bonds (for some Summer Tanagers, Baltimore Orioles, Rose-breasted Grosbeaks) and intraspecific flocks (for certain icterids and fringillids). The passerines that formed intraspecific feeding flocks were often associated with concentrated local food sources in man-disturbed areas. These foods included

TABLE 4

INDIVIDUAL FORAGING OR FEEDING RECORDS ON BARRO COLORADO DURING RAIN[1]

	Light[2] (5 hours)	Moderate (3½ hours)	Heavy (1½ hours)
RESIDENTS			
Orange-chinned Parakeet		2	
Collared Aracari	7		
Tropical Kingbird		1	
Social Flycatcher		1	
Short-crested Flycatcher			1
Green Honeycreeper	2	1	
Fulvous-vented Euphonia	4	1	
Plain-colored Tanager	26	4	
Golden-masked Tanager	1	3	
Blue-Gray Tanager	3	4	3
Palm Tanager	9	8	5
Crimson-backed Tanager	1		
TOTALS	53	25	
MIGRANTS			
Olive-sided Flycatcher		1	
Eastern Wood Pewee		2	2
Tennessee Warbler	1	8	
Yellow Warbler	7	2	
Chestnut-sided Warbler	1	5	
Bay-breasted Warbler	2	1	
Northern Waterthrush	1		
Summer Tanager	2	4	2
Rose-breasted Grosbeak		4	
TOTALS	14	27	

[1] All food sources (mostly October and November 1968). A 2×2 Chi-square test of residents and migrants in light and moderate rains showed a highly significant difference between the activity of the two avifaunas ($p < 0.001$).

[2] Definition of intensities of rainfall: Light, a drizzle or fine rain, does not require one to seek shelter; moderate, requires one to seek shelter or to wear rain gear; heavy, a torrential downpour, usually of short duration.

cultivated fruiting and flowering trees for icterids and grain fields for fringillids. At such superabundant resources the competition, intraspecifically or with residents, was negligible.

Migrants also formed interspecific associations with the mixed flocks of residents. In most cases, the migrants were attracted by the residents; the migrants were the active joiners. Moynihan (1962) made the same observation but did not directly discuss the basis of this one-way relationship between migrants and residents. As the joining behavior causes migrants and residents to share foods, competition might result when resources are scarce. In aggressive encounters at food sources, migrants were usually subordinate to residents (Leck, 1972) through dominance hierarchies based on size with the larger species dominant (Leck, 1970;

Wolf, 1970). Since migrants are often small (e.g. Parulidae) or belong to families that have larger representatives in the tropics (e.g. orioles and thrushes), they are more likely to lose aggressive encounters. Their small biomass would also reduce their competitive impact.

Territorial behavior was noted in only two migrants, the Northern and Louisiana Waterthrushes, which defend individual interspecific feeding areas along small montane streams. Where allopatric they also exhibit territorial tendencies (Eaton, 1953; Schwartz, 1964). The territoriality may be necessary partly because few streams are available in the wintering areas.

DISCUSSION

In Panama the impact of migrants increases at 6,000 feet elevation. This increase has been subjectively appreciated by previous workers, with several suggestions of its significance. Willis (1966) noted that in the man-disturbed habitats such as the highland coffee fincas the resident birds have "practically disappeared," leaving unfilled areas for migrants. In the last 50 years, agriculture in the highlands has had many detrimental effects on many native birds and mammals (Bennett, 1968), but migrants might benefit from the resources available in the open habitats (Slud, 1960: 144). Widely-spaced natural habitat patches of highlands might also provide areas too small to be filled by residents, and the mobile migrants could select such places where resident competitors are fewer than in a large continuous habitat, such as a lowland rainforest. Highlands may also be attractive because they are more like the breeding habitats of the migrants (Brosset, 1968). Workers in other tropical regions also describe the migrant preference for higher elevations (e.g. in Thailand, B. King, pers. comm.) and concomitantly their apparent avoidance of mature lowland forests, as in Malaysia (Ward, 1969).

A review of the data suggests that the migrants generally do not compete strongly with residents in Panama, at least within natural habitats. These data include: (1) the comparatively low fruit exploitation rates of migrants in the clearing on Barro Colorado Island, (2) the preference of frugivorous migrants for areas of food superabundance, either in man-disturbed areas or in the highlands, and (3) the low positions of migrants in dominance hierarchies. The impact of migrant exploitation might sometimes be important during marked food shortages, as in the wet season (Leck, 1970) or during peak migration periods. Differences in migrant and resident feeding efficiencies may also be reflected in the dichotomy of rain foraging in the wet season. More efficient residents may be able to avoid foraging during the rainy spells, while the migrants,

being less efficient and/or of reduced weights from migration, are obliged to continue feeding through the day, even during unfavorable weather. Low efficiency could result from problems in food recognition, especially for young migrants.

Considering the food recognition problems of migrants, their partial dependence on residents, and their low position in dominance hierarchies, it is likely that they, rather than native species, would suffer during any food shortage competition. In recent years the migrants are more able to avoid such competition by exploiting the superabundance of fruit in man-disturbed areas.

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SUMMARY

The relative population sizes and exploitation levels of frugivorous migrant were studied during several seasons in Panama and the Canal Zone. In the lowlands migrants were responsible for less than 10 percent of the total avian-fruit utilization. Their importance increased to 45 percent at 6,000 feet elevation. In both regions migrants appeared to frequent such areas of fruit superabundance as man-disturbed areas and natural habitat patches. During rainy periods migrants remained more active in foraging than residents.

LITERATURE CITED

BENNETT, C. F. 1968. Human influences on the zoogeography of Panama. Ibero-Americana, 51: 1–112.

BROSSET, A. 1968. Localisation ecologique des Oiseaux migrateurs dans la foret equatoriale du Gabon. Biol. Gabonica, 4: 211–216.

EATON, S. W. 1953. Wood warblers wintering in Cuba. Wilson Bull., 65: 169–175.

EISENMANN, E. 1955. The species of Middle American birds. Trans. Linnaean Soc. New York, vol. 7.

GALINDO, P., AND E. MENDEZ. 1965. Banding thrushes and catbirds at Almirante, Panama. Second year of observations. Bird-Banding, 36: 233–239.

LECK, C. F. 1969. Palmae: hic et ubique. Principes, 13: 80.

LECK, C. F. 1970. The seasonal ecology of fruit and nectar eating birds in lower Middle America. Unpublished Ph.D. dissertation, Ithaca, New York, Cornell Univ.

LECK, C. F. 1972. Seasonal changes in feeding pressures of fruit and nectar eating birds in the neotropics. Condor, 74: 54–60.

LECK, C. F., AND S. HILTY. 1968. A feeding congregation of local and migratory birds in the mountains of Panama. Bird-Banding, 34: 318.

MILLER, A. H. 1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. Univ. California Publ. Zool., 66: 1–78.

MOREL, G., AND F. BOURLIERE. 1962. Relations ecologiques des avifaunas sedentaire et migratrice dans une savane sahelienne du bas Senegal. La Terre et la Vie, 4: 371–393.

MOYNIHAN, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Coll., 143.

SCHWARTZ, P. 1964. The northern waterthrush in Venezuela. Living Bird, 3: 169–184.

SLUD, P. 1960. The birds of finca "La Selva", Costa Rica: a tropical wet forest locality. Bull. Amer. Mus. Nat. Hist., 121.

WARD, P. 1969. The annual cycle of the Yellow-vented Bulbul *Pycnonotus goiavier* in a humid equatorial environment. J. Zool., 157: 25–45.

WILLIS, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird, 5: 187–231.

WOLF, L. L. 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds, Condor, 72: 1–14.

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APPENDIX: SCIENTIFIC NAMES OF THE SPECIES MENTIONED

Sulphur-winged Parakeet (*Pyrrhura hoffmanni*)
Orange-chinned Parakeet (*Brotogeris jugularis*)
Emerald Toucanet (*Aulacorhynchus prasinus*)
Collared Aracari (*Pteroglossus torquatus*)
Acorn Woodpecker (*Melanerpes formicivorus*)
Red-crowned Woodpecker (*Centurus rubricapillus*)
Fork-tailed Flycatcher (*Muscivora tyrannus*)
Eastern Kingbird (*Tyrannus tyrannus*)
Tropical Kingbird (*Tyrannus melancholicus*)
Gray Kingbird (*Tyrannus dominicensis*)
Short-crested Flycatcher (*Myiarchus ferox*)
Social Flycatcher (*Myiozetetes similis*)
Olive-sided Flycatcher (*Nuttallornis borealis*)
Eastern Wood Pewee (*Contopus virens*)
Mountain Elaenia (*Elaenia frantzii*)
White-throated Robin (*Turdus assimilis*)
Clay-colored Robin (*Turdus grayi*)
Mountain Robin (*Turdus plebejus*)
Wood Thrush (*Hylocichla mustelina*)
Swainson's Thrush (*Hylocichla ustulata*)
Long-tailed Silky-flycatcher (*Ptilogonys caudatus*)
Red-eyed Vireo (*Vireo olivaceus*)
Green Honeycreeper (*Chlorophanes spiza*)
Red-legged Honeycreeper (*Cyanerpes cyaneus*)
Blue Dacnis (*Dacnis cayana*)
Bananaquit (*Coereba flaveola*)
Tennessee Warbler (*Vermivora peregrina*)
Yellow Warbler (*Dendroica aestiva*)
Chestnut-sided Warbler (*Dendroica pensylvanica*)
Bay-breasted Warbler (*Dendroica castanea*)
Northern Waterthrush (*Seiurus noveboracensis*)
Louisiana Waterthrush (*Seiurus motacilla*)
Kentucky Warbler (*Oporornis formosus*)
Canada Warbler (*Wilsonia canadensis*)
Baltimore Oriole (*Icterus galbula*)
Fulvous-vented Euphonia (*Tanagra fulvicrissa*)
Plain-colored Tanager (*Tangara inornata*)
Golden-masked Tanager (*Tangara larvata*)
Silver-throated Tanager (*Tangara icterocephala*)
Blue-gray Tanager (*Thraupis episcopus*)
Palm Tanager (*Thraupis palmarum*)
Crimson-backed Tanager (*Ramphocelus dimidiatus*)
Summer Tanager (*Piranga rubra*)
Scarlet Tanager (*Piranga olivacea*)
Flame-colored Tanager (*Piranga bidentata*)
Streaked Saltator (*Saltator albicollis*)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)
Yellow-throated Brush-Finch (*Atlapetes gutturalis*)