

AVIAN FRUGIVORE ACTIVITY IN RELATION TO FOREST LIGHT GAPS

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SEVERAL species of North American birds feed heavily on small, fleshy fruits during the summer breeding season and even more intensively during fall migration (Thompson and Willson, 1979). The peak fruiting times for several eastern deciduous-forest plant species whose fruits are consumed and seeds dispersed by these frugivores correspond well with the time of maximum frugivore migration (Thompson and Willson, 1979). Experiments have shown that fruit removal rates are generally lower in forest interior than on forest edges or in light gaps (openings in the canopy, usually caused by a tree- or branch-fall) (Thompson and Willson 1978). The present study explores the extent of avian preferences for light gaps during fall migration in east-central Illinois, comparing birds of different feeding habits (emphasizing frugivores). Comparative data from spring migration in the same locale are presented as a partial control, in that many of the same bird species are present but fruits are not. Further comparisons are made with samples from lowland and highland neotropical forests, in which frugivory is common and avian movement patterns are quite different.

STUDY AREA AND METHODS

The principal study area was Trelease Woods, a 22-ha woodlot located just northeast of Urbana (Champaign Co.), Illinois. Principal tree species include sugar maple (*Acer saccharum*), elm (*Ulmus*), white ash (*Fraxinus americana*), basswood (*Tilia americana*), oaks (*Querc-*

us spp.), and hackberry (*Celtis occidentalis*); the understory includes pawpaw (*Asimina triloba*) and spicebush (*Lindera benzoin*) as well (see also Boggess 1964, Pelz and Rolfe 1977).

Comparative data were obtained from Panamanian forest in both wet and dry seasons. Lowland forest sites were located on Achiote Road on the Caribbean side of the isthmus (dry season only), Barro Colorado Island and the Pipeline Road in the central part of the isthmus (dry season), and Rancho Ron in Darien Province (wet season). Highland sites at about 1400 m near El Volcán, Chiriqui province were sampled in both seasons and a dry-season sample came from disturbed forest above Cerro Punta (at about 2000 m).

Comparisons are drawn from mist-netted samples of avian populations in the various sites. In all cases, 12-m mist nets of 30 mm and 35 mm mesh size were placed in light gaps of sufficient size to contain the extended net and in adjacent forest interior. In general, Trelease nets were open from dawn to late morning, 3 days a week; Panamanian nets from dawn to midday (or sometimes dusk) on 3 consecutive days (only 2 at Rancho Ron) at each site. Spring and fall mistnet sites in Trelease were identical in 1978-79, to facilitate seasonal comparisons. Fifteen-minute visual censuses of understory birds in gaps and interior of Trelease Woods (N = 37 paired censuses) corroborated the mist-net samples.

Data were collected from Trelease by RSC from 8 September to 19 October 1977 and from 29 April to 30 May 1978, and by EAP from 21 August to 21 October 1978 and from 28 April to 22 May 1979. MFW obtained the Panamanian data in January and February (dry season)

and July and August (wet season) 1979. A small sample came from mixed conifer-deciduous forest in Itasca State Park, Minnesota (10 nets, 105 mist-net hours) on 14 and 16 August 1978, just as migration was beginning. A similar attempt at this site in July 1978 and again in early September 1979 yielded too few birds to analyze.

An indication of sampling effort is obtained from the number of nets used and the total of mist-net hours (evenly divided between gap and interior) accumulated: Trelease, fall 1977, 6 nets, about 430 mnh; spring 1978, 6 nets, mnh not known; fall 1978, 14 nets, 1456 mnh; spring 1978, 14 nets, 560 mnh; Achiote Road, 10 nets, 100 mnh; Pipeline Road, 8 nets, 145 mnh; Barro Colorado Island, 10 nets, 182 mnh; Rancho Ron, 10 nets, 132 mnh; Cerro Punta, 8 nets, 156 mnh; El Volcán Site 1, 10 nets, 202 mnh (wet and dry seasons); El Volcán Site 2, 10 nets, 152 mnh (wet season). Capture rates ranged from 0.23 to 0.74 birds per mist-net hour, with no marked differences between regions.

Illinois birds were assigned to guilds on the basis of information in Beal (1915), Graber and Graber (1970, 1971), Martin *et al.* (1951), and our own observations; Panamanian birds were assigned in consultation with J. R. Karr. Birds classified as frugivores have a diet estimated to be composed of at least 25% fruits (during the fall for temperate species); this class thus includes species that eat a mixed diet of fruit and invertebrates (or small vertebrates) as well as those that are predominantly frugivorous. Guild assignments and some scientific names are indicated in the Appendix.

In all cases the 5% level of significance was used for statistical tests.

RESULTS

North-central United States.—In Trelease Woods in the fall, frugivores, as a group, were netted (Table 1) and seen more often in light gaps than in forest interior. This resulted primarily from the distributions of Swainson's thrushes and robins. Foliage-gleaning insectivores, collectively, and 3 species in particular, were more active in gap areas. Finches, which are typically granivorous in the fall, were also found more frequently in gaps, due in part to the distribution of white-throated sparrows (*Zonotrichia albicollis*).

Thus 3 major feeding guilds, taken collective-

ly, and therefore the entire sample of birds captured or observed, were more common in light gaps. Overall, 7 of 12 species captured or seen sufficiently often to test their microhabitat distribution showed such a preference in fall.

Twenty-three of the 29 birds captured in August at Itasca were captured in light gaps; all were insectivores.

Birds that are frugivores and granivores in the fall switch to insects and other invertebrates in spring, but we continue to distinguish them for the sake of seasonal comparisons. "Frugivores" and insectivores (but not "granivores") preferred gaps in spring as well as in fall. Several species were found most often in gaps (Table 1); 8 of 11 species with sufficient sample sizes preferred gaps.

Panama.—Only at El Volcán in the dry season were there any significant differences in the distribution of all birds between gap and interior, and only at Cerro Punta where the forest was much disturbed and gaps were less clearly defined were frugivores found more often in gaps (Table 2). Even if all sites are pooled to increase sample sizes (total = 507 birds), there are no differences between gaps and interior. Thirteen species had samples of at least 10 individuals (from all sites); none of these, including 3 frugivores (black-faced solitaire, red-capped manakin, white-ruffed manakin), showed preference for either gap or interior. The results were unchanged if only species whose diet is almost entirely fruit ($\geq 75\%$) are considered.

DISCUSSION

We can approach several questions with these results. First, why do so many migrant birds in Trelease seem to prefer light gaps? Clearly the reasons need not be the same for all species. The frugivores (in fall) might seek out gaps that present edible fruits. In fall 1978, two nets placed in gaps with large quantities of fruit nearby caught 13 and 19 frugivores, 3 gap nets near moderate amounts of fruits caught 7-12 frugivores, and 2 gap nets with little or no fruit nearby caught 3-5 frugivores. Interior nets with fruit present or located between adjacent light gaps had the highest capture rates of all interior nets (9 and 10 birds compared to 1-7 birds). But these were not the most favored sites in spring. This would seem to suggest that the presence of fruit contributes to the birds' spatial preferences. However, the preferences of "fru-

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givores," and indeed of all birds, for light gaps seems as marked in spring, when no fruit is available, as in fall.

Birds feeding on insects, especially foliage insects, may be found in light gaps for several reasons. Canopy foragers may simply follow the canopy as it dips groundward around the edges of the gap. Insects may be more active, abundant, or visible in the well-lit gaps than in the interior.

Second, why do the Panamanian forest birds show less preference for light gaps than north temperate migrants? That these results may be generally true is suggested by preliminary but similar results of Willson and Moriarty (1976) in Costa Rica. However, Schemske and Brokaw (1981) in an extensive sample from the Pipeline Road found 8 species (of over 31 tested) with a significant or nearly significant preference; 5 of these preferred gaps. Of these 5, one (*Cyanocopsa cyanoides*) is a partial frugivore. Two species associated with gaps in their study were not so in ours.

Surveys of the distribution of fleshy fruits along our Panamanian mist nets indicated that light gaps contained no fruit concentrations such as can be found in Trelease Woods. Several plant species bore small, fleshy fruits, but most of them were widely scattered in the forest interior, and no association was noted between the presence of a plant bearing ripe fruit and the capture of frugivores in an adjacent net. The paucity of fruits in light gaps may help explain the even distribution of frugivores but does not further the explanation for other birds.

Two possibilities may be suggested: Tropical insects are not more readily captured in light gaps, although temperate-zone insects may be. A priori, this seems a dubious possibility. Many tropical birds, such as antwrens, forage in thick foliage tangles such as are found at the periphery of light gaps. Perhaps more likely is that some factor may prevent tropical birds from using light gaps as much as their northern counterparts. It seems possible that predators might select for behavior patterns in birds that minimize exposure. This could take the form of continued cover-seeking and/or a tendency not to concentrate activity in any one place. We know of no detailed studies that firmly establish the comparative risks of capture for fledged forest birds, so the suggestion must remain tentative. Conceivably, the energy demands for southward migration are so much greater (for in-

stance, small birds may increase their body weights 50-100% by fat deposition just prior to migration, Clark 1979) than for subsistence in the tropical forests that the use of light gaps is advantageous, despite any risk of predation. This then raises the question about the energy sources for northward migration from the tropics back to temperate regions; again fruits are apparently important sources for some birds (e.g. Fry *et al.* 1970, Morton 1971).

Because Trelease is a woodlot surrounded by fields, it might be argued that the birds caught in gaps are really forest-edge birds that wandered into the woods. Indeed, several species, such as the white-throated sparrow, hardly qualify as birds of the forest habitat. Several of the tropical netting sites were also located short distances from clearings or roads where non-forest birds were found (Chiriqui, Pipeline Road). Yet the tropical sites seldom exhibited avian preferences for gaps, suggesting either that tropical forest-edge birds that wander into forest seldom use gaps or that they seldom wander there at all. In either case, the observation that tropical birds seem to use light gaps less than temperate birds still stands.

These results have several implications. Because many frugivorous birds are seed dispersers, the preferences of temperate deciduous forest birds for light gaps will tend to concentrate seeds of certain species in these places, whereas this may not be true in Panamanian forests (see also Denslow 1978). The spatial patterns of secondary succession and details of plant community structure must differ between regions as a result, and the life histories of certain plant species must also differ; such consequences require further study (Thompson and Willson 1978, Denslow 1978). The importance of habitat patches for population and community ecology was summarized by Wiens (1976).

For the ecology and management of avian wildlife in temperate forests, the utility of light gaps and of the plants that are dispersed among them should be clear. It remains to be seen how the birds might fare in the absence of such resources; the energy demands of migration are high and immediate, and sometimes the ability to find food rapidly may be critical to success of the journey. The ecology of migration has been so little studied, at both the species and the community level, that virtually nothing is known. One purpose of this report is to call attention to the interesting differences in dis-

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tribution and the need for more information.

SUMMARY

Mist-net samples of birds using light gaps and adjacent forest interior during fall and spring migration show that birds of several feeding guilds and a number of species in temperate deciduous forest are found more often in light gaps than in forest interior. Comparative samples from various Panamanian forests show no such general predilection. Although there are implications of this observation for the ecologies of both birds and bird-dispersed plants, the main focus of this study is descriptive, calling attention to phenomena of potential importance at several levels of organization.

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TABLE 1. Trelease Woods: Number of birds (by feeding guild) caught in light-gap and forest-interior mist nets, 1977-1979. Significant differences (X^2 when $N \geq 25$, binomial test if $N < 25$; $p \leq 0.05$) are marked with an asterisk. Data for single species are shown when $N \geq 10$ in at least one sampling period.

FEEDING GUILD	FALL 1977		FALL 1978		SPRING 1978		SPRING 1979	
	GAP	INTERIOR	GAP	INTERIOR	GAP	INTERIOR	GAP	INTERIOR
Frugivores	62 *	32	76 *	37	12	7	54 *	33
Swainson's thrush	11	8	30 *	11	2	1	19	17
Hermit thrush	22	18	16	13	2	0	4	1
American robin	17 *	3	3	0	0	0	7	4
Wood thrush	0	2	9	4	0	0	6	0
Foliage-gleaning Insectivores	37 *	0	59 *	18	54 *	15	102 *	13
Nashville warbler	3	0	1	0	4	1	19	2
Magnolia warbler	13 *	0	17 *	2	20 *	4	15	0
Tennessee warbler	1	0	11 *	1	7	0	17	2
Canada warbler	1	0	10 *	3	11	4	6	0
Palm warbler	0	0	0	0	3	0	17	7
Ruby-crowned kinglet	11 *	0	1	0	0	0	3	0
Other insectivores	10	11	65	46	22	10	35	10
Ovenbird	2	9	41	33	1	5	14	5
Black-and-white warbler	3	0	11	9	3	1	2	1
American redstart	0	0	3	2	12 *	3	5	0
Granivores	25 *	0	15 *	2	5	6	27	26
White-throated sparrow	19 *	0	4	0	2	0	0	0
Indigo bunting	0	0	0	0	3	6	14	17
All Birds	137 *	44	232 *	109	98	39	224 *	91

TABLE 2. Summary of Panama forest data (totals include captures from other guilds as well).

	GAP		INTERIOR			GAP		INTERIOR	
Achiote Road					Rancho Ron				
frugivores	7		13		frugivores	5		2	
insectivores	20		13		insectivores	13		10	
all birds	27		27		all birds	18		12	
Barro Colorado Island					El Volcán (dry season)				
frugivores	11		12		frugivores	11		8	
insectivores	15		9		insectivores	47		27	
all birds	26		21		all birds	58	*	36	
Cerro Punta					El Volcán (wet season)				
frugivores	19	*	7		frugivores	4		3	
insectivores	29		30		insectivores	23		30	
all birds	60		56		all birds	27		33	
Pipeline Road					El Volcán (wet season)				
frugivores	6		4		frugivores	7		4	
insectivores	21		22		insectivores	21		21	
all birds	27		26		all birds	28		25	

APPENDIX 1. Principal guild assignments of captured birds.

A. Trelease Woods

Frugivores:

Common flicker	<i>Colaptes auratus</i>
Swainson's thrush	<i>Catharus ustulatus</i>
Hermit thrush	<i>C. guttatus</i>
Gray-cheeked thrush	<i>C. minimus</i>
Veery	<i>C. fuscescens</i>
Wood thrush	<i>Hylocichla mustelina</i>
American robin	<i>Turdus migratorius</i>
Gray catbird	<i>Dumetella carolinensis</i>
Brown thrasher	<i>Toxostoma rufum</i>
Red-eyed vireo	<i>Vireo olivaceus</i>
Yellow-rumped warbler	<i>Dendroica coronata</i>

Foliage-gleaning insectivores: most parulids and sylvids, except as indicated below or in Table 1.

Other insectivores: flycatchers, wrens, most woodpeckers, nuthatches, brown creepers (*Certhia familiaris*), black and white warbler (*Mniotilta varia*), American redstart (*Setophaga ruticilla*), ovenbird (*Seiurus aurocapillus*), northern waterthrush (*Seiurus noveboracensis*).

Granivores: mostly fringillids.

Few birds were classified in other guilds.

B. Panama (capture site indicated by initials)

Frugivores:

Ruddy quail-dove	<i>Geotrygon montana</i>	EV
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Rufous motmot	<i>Baryphthengus martii</i>	AR	nightingale thrush	<i>C. gracilirostris</i>	CP
Emerald toucanet	<i>Aulacorhynchus prasinus</i>	EV	Scarlet-rumped cacique	<i>Cacicus uropygialis</i>	AR
Blue-crowned manakin	<i>Pipra coronata</i>	PR,RR	Lemon-browed tanager	<i>Chlorothraupis olivacea</i>	RR
Red-capped manakin	<i>P. mentalis</i>	AR,PR, BCI	Red-throated ant-tanager	<i>Habia fuscicauda</i>	AR
White-ruffed manakin	<i>Corapipo alera</i>	EV	Buff-throated saltator	<i>Saltator maximum</i>	EV
Golden-collared manakin	<i>Manacus vitellinus</i>	AR	Streaked saltator	<i>S. albicollis</i>	EV
Mountain Elaenia	<i>Elaenia frantzii</i>	CP	Blue-black grosbeak	<i>Cyanocompsa cyanooides</i>	EV
Olive-striped flycatcher	<i>Mionectes olivaceus</i>	AR,RR, EV	Yellow-thighed finch	<i>Pseliophorus tibialis</i>	CP
Ochre-bellied flycatcher	<i>Pipromorpha oleaginea</i>	AR,PR, BCI	Black-striped sparrow	<i>Arremonops controstris</i>	EV
Black-faced solitaire	<i>Myadestes metanops</i>	EV,CP			
White-throated robin	<i>Turdus assimilis</i>	EV			
Mountain robin	<i>T. plebejus</i>	CP			
Wood thrush	<i>Hylocichia mustelina</i>	BCI,EV			
Swainson's thrush	<i>Catharus ustulatus</i>	EV			
Ruddy-capped nightingale thrush	<i>C. frantzii</i>	CP			
Black-billed					

Insectivores: For the sake of this comparison, wood-creepers, wood-warblers, wrens, antbirds, furnarids, hummingbirds, certain flycatchers and finches not listed above were treated in this broad classification.

Few birds were classified in other guilds, except at Cerro Punta, where granivorous slaty finches (*Spodiornis rusticus*) were common when bamboo was fruiting.