INFLUENCE OF RESOURCE ABUNDANCE ON USE OF TREE-FALL GAPS BY BIRDS IN AN ISOLATED WOODLOT

JOHN G. BLAKE[1] AND WILLIAM G. HOPPES[2]

Department of Ecology, Ethology, and Evolution, 606 East Healey Street, University of Illinois, Champaign, Illinois 61820 USA

ABSTRACT.—The occurrence of birds in forest understory and tree-fall gaps during spring and fall migration periods was determined in an isolated woodlot. We used mist-net captures to test the hypothesis that birds are attracted to gaps because of higher resource levels. We captured 1,010 birds (74 species) in spring and 458 (44 species) in fall. Total captures and captures per net were higher ($P < 0.001$) in gaps during spring and fall. Mean number of species per net was higher in gaps ($P < 0.001$) during both seasons, but total species in gaps (69 spring, 43 fall) was not significantly higher than in forest understory (60 spring, 28 fall). Of 44 species represented by adequate sample sizes ($n > 5$) in spring, 9 were significantly ($P < 0.05$) more common in gaps and 2 were more common in forest understory. Nine of 17 species were captured more often ($P < 0.05$) in gaps during fall. During spring, flycatchers, ground insectivores, foliage insectivores, and granivore-omnivores were captured more frequently ($P < 0.05$) in gaps. Flycatchers showed no difference in fall, but other trophic groups, including frugivores, were captured more frequently ($P < 0.05$) in gaps than in forest understory sites. Bark foragers showed no statistical preference for gaps or forest understory in spring or fall. Total species per net and total captures per net correlated positively ($P < 0.05$) with density of foliage in the lower canopy and negatively with density of upper canopy foliage in both spring and fall. Total species and captures correlated positively ($P < 0.05$) with insect abundance in spring and with fruit abundance in fall. Foliage insectivores correlated positively with low canopy foliage and insect abundance in both spring and fall. Captures of frugivores correlated with fruit abundance in fall. These data support the hypothesis that birds are attracted to tree-fall gaps because of higher resource abundance and provide further evidence of the importance of habitat heterogeneity to the structure and composition of bird communities. *Received 7 November 1984, accepted 28 October 1985.*

GAPS caused by tree falls contribute to the creation of a habitat mosaic in many forests (Williamson 1975; Hartshorn 1978; Whitmore 1978; Runkle 1981, 1982; Brokaw 1985). Tree-fall gaps ["a vertical 'hole' in the forest extending to within 2 m of the forest floor" (Brokaw 1982)] influence abundance and distribution of bird species by maintaining habitat heterogeneity and by affecting abundance and distribution patterns of food resources (e.g. fruit and insects). Resource levels may be higher in gaps because of greater primary productivity associated with increased light levels (Fogden 1972, Halle et al. 1978). Previous studies in east-central Illinois (Willson et al. 1982, Martin and Karr 1986) have demonstrated differences in assemblages of birds captured in forest gaps and understory. Results of these studies suggest that birds might be attracted to gaps because of higher resource levels. Here, we test the prediction that abundance of individuals in gaps and forest understory correlates with abundance of resources in these locations. We used mist nets to obtain concurrent samples of birds in gaps and forest understory sites and compared number and species composition of captures with estimates of insect and fruit abundance and with measures of vegetation structure for the same sites.

Migration is energetically expensive, and many birds must replenish fat reserves periodically (Berthold 1975, Graber and Graber 1983, Walsberg 1983). Food supplies often are low or unpredictable during migration (Walsberg 1983), particularly in spring when migrants are moving toward areas where local weather conditions may be severe and unpredictable. Find-

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[1] Present address: Department of Zoology, Birge Hall, University of Wisconsin, Madison, Wisconsin 53706 USA.

[2] Present address: Center for Earth and Environmental Science, Hudson Hall 102, State University of New York, Plattsburgh, New York 12901 USA.

ing adequate food after a flight may be difficult because the landing area often is unknown to migrants. Consequently, it would be advantageous for birds to recognize and quickly select foraging sites that are profitable (Martin and Karr 1986). This may be particularly true for migrants in east-central Illinois, where natural habitat is limited and exists as isolated patches in an agricultural setting (Blake 1986). Recent work by Graber and Graber (1983) demonstrated that migrant warblers in spring experience a net loss of energy while foraging in woodlots in east-central Illinois. By demonstrating differences in resource levels between gaps and forest understory sites, and by demonstrating correlations between capture frequency and resource level, we support the prediction that during migration birds select as foraging sites microhabitats with abundant food resources.

STUDY AREA AND METHODS

Study site.—We mist-netted birds in William Trelease Woods, an upland forest tract of about 24 ha located 6.5 km northeast of Urbana (Champaign County), Illinois. Principal trees in the woods are sugar maple (*Acer saccharum*), hackberry (*Celtis occidentalis*), white ash (*Fraxinus americana*), slippery elm (*Ulmus rubra*), basswood (*Tilia americana*), red oak (*Quercus rubra*), and buckeye (*Aesculus glabra*). The understory supports a variety of species, including young individuals of the above species, pawpaw (*Asimina triloba*), and spicebush (*Lindera benzoin*).

Many species present in Trelease Woods produce fruits that are eaten by birds in late summer and fall. These include spicebush, hackberry, Virginia creeper (*Parthenocissus quinquefolia*), wild grape (*Vitus vulpina*), moonseed (*Menispermum canadensis*), catclaw (*Smilax hispida*), poison ivy (*Rhus radicans*), and wahoo (*Euonymus atropurpureus*).

Birds.—We used mist nets (12 m length, 2.6 m height, 36 mm mesh) to sample birds using the lower levels (bottom 2-3 m) of gaps and forest understory during spring and fall 1983. We believe that the advantages gained by simultaneous sampling of all sites outweigh any biases associated with mist-net samples (Karr 1979, Martin and Karr 1986; but see Remsen and Parker 1983). Also, comparisons with previous tree-fall gap studies are facilitated because similar techniques were used (Schemske and Brokaw 1981, Willson et al. 1982, Martin and Karr 1986). Six nets were placed in gaps (1/gap) and 6 in forest understory. Gap nets were positioned to minimize visibility while still remaining within the gaps. We did not place nets in forest understory between gaps that were less than 40 m apart or within 20 m of a gap edge. Although exact age of the gaps is not known, all were well established and at least 3-5 yr old.

We netted birds 3 days/week, except when rain or strong winds precluded use of nets, from about 15 min before sunrise until about noon. We standardized netting effort among days to avoid problems associated with diurnal variability in capture rates (Karr 1981). We netted birds on 18 days in spring (19 April to 5 June) and on 24 days in fall (23 August to 31 October). Nets were checked every hour, and captured birds were identified, sexed (when possible), weighed, banded with U.S. Fish and Wildlife Service aluminum leg bands, and released at point of capture.

We compared the number of captures in gap and forest understory nets using Chi-square tests (for sample sizes ≥ 30) or Fishers Exact Test (for $n < 30$; Sokal and Rohlf 1981). We correlated number of captures per net with measures of habitat structure and resource abundance (see below) using Spearman's rank correlation (Sokal and Rohlf 1981).

We divided species into six major trophic groups in spring (flycatchers, ground insectivores, bark foragers, foliage insectivores, omnivore-granivores, and nectarivores) and seven in fall (above six plus frugivores) based on literature (Martin et al. 1951, Willson 1974, Willson et al. 1982) and personal observations (see Appendix). Nectarivores were represented by one species (Ruby-throated Hummingbird, *Archilochus colubris*), and we did not include nectarivores in the analyses of trophic groups. We categorized frugivores as primary [those that depend heavily on fruit, i.e. more than 75% of foraging observations in fall (Hoppes pers. obs.)] and secondary frugivores [those that consume fruit regularly but less often than primary frugivores, i.e. 25-50% of foraging observations in fall (Hoppes pers. obs.)] and compared numbers of captures of all frugivores and number of captures of primary and secondary frugivores separately. Because considerable attention has been placed on the use of gaps by frugivores in fall (e.g. Thompson and Willson 1978, 1979), we also examined use of gaps and forest understory during spring by species that are frugivorous in fall.

Vegetation.—We recorded vertical distribution of vegetation at each net site following the methods of Karr (1971). Presence or absence of vegetation in each of 14 height intervals was noted at 40 points per net (Fig. 1). Height intervals (meters) were 0-0.3, 0.3-0.9, 0.9-1.5, 1.5-2.1, 2.1-2.7, 2.7-3.4, 3.4-4.0, 4.0-4.6, 4.6-6.1, 6.1-9.1, 9.1-12.2, 12.2-15.2, 15.2-18.3, and >18.3. Percentage cover for a given height interval was calculated as the percentage of all points with vegetation present at that height. We sampled vegetation profiles each week in spring and once every three weeks in fall, when foliage distributions change less rapidly.

We recorded the number of trees [individuals with a diameter at breast height (DBH) of at least 7.6 cm]

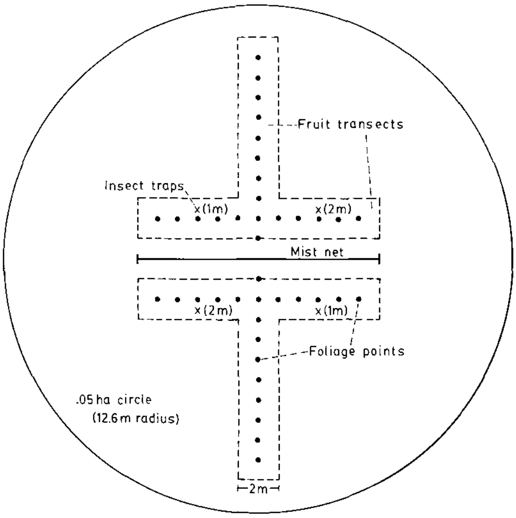

Fig. 1. Sampling design for gap and forest understory nets.

in a 0.05-ha circle (12.6 m radius) centered on the middle of each net (Fig. 1). Trees were identified and assigned to 1 of 7 size classes: 7.6–15, 15–23, 23–38, 38–53, 53–69, 69–84, and 84–102 cm DBH (James and Shugart 1970).

Fruit-producing shrubs and vines were sampled along 2-m-wide transects (80 m^2 total/site) at each net site (Fig. 1). All individuals that produced fruit were marked, and numbers of ripe and unripe fruit were recorded at biweekly intervals in fall. No fruits were present during spring.

Because we sampled foliage, trees, and fruit up to 12.6 m from the center of each gap net (Fig. 1), our samples sometimes included area beyond gap edges. Thus, although gaps were defined as a "vertical hole" in the vegetation, vegetation above 2 m could be recorded at gap nets.

Insects.—We used 15 × 15-cm plates of plexiglass coated with a thin layer of Tree Tanglefoot (Cody 1980, Hutto 1980) to sample insect abundance. Plates were suspended at about 1 and 2 m at four points around each net (Fig. 1), for a total sampling area of 1,800 cm^2 (4 plates, 225 cm^2/side) at each net site. Traps were uncovered at dawn and checked shortly after noon on 5 days in spring and 6 in fall. Captured insects were counted, identified to order, and measured to the nearest millimeter. Traps were covered with a thin sheet of plastic when not in use. We recognize that our data are not a direct measure of the availability of insects eaten by all insectivorous birds. However, we assume that the densities of insects caught are correlated with densities of insectivorous bird food and that the results provide a basis for comparing insect availability among sites (Hutto 1980). Efficiency of sticky traps varies with such factors as wind speed (Johnson 1950) and position of board relative to vegetation (Login and Pickover 1977). We minimized effects of these factors by hang-

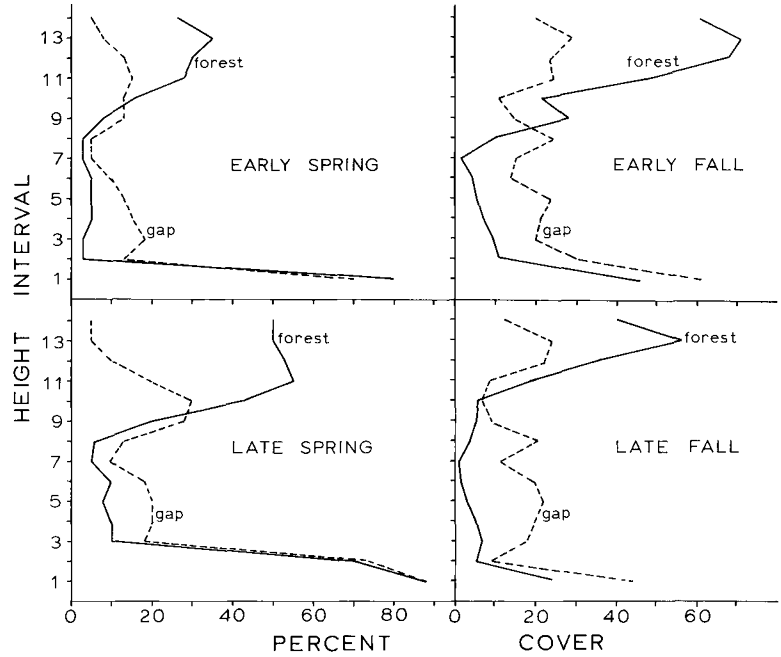

Fig. 2. Foliage profiles for gap and forest understory sites.

ing all boards in the same position for each sampling period and by not sampling on windy days.

Prior to testing for differences between gap and forest understory sites, we tested the data on vegetation and resource abundance for normality (Shapiro-Wilks test). We used a Mann-Whitney test (standard normal deviate calculated, SND) when there was a significant departure from normality and t-tests when data did not depart from normal distribution. We tested variances for equality (F-test) and used a t' test (Sokal and Rohlf 1981) if variances were not equal.

RESULTS

Vegetation.—Forest understory sites were dominated by sugar maple, basswood, and elm; gaps were dominated by oak, ash, and hackberry. Small trees (7.6–15 cm DBH) were dominant in gaps, and average number per net site was higher in gaps than in forest locations. All other size classes were more abundant in forest sites than in gaps, but total tree density was not significantly higher ($t = 1.41$, $P < 0.40$) in understory sites ($\bar{x} = 56$ trees/0.05 ha) than in gaps ($\bar{x} = 48$/0.05 ha). Differences in basal area per size class were pronounced between gaps and understory, and average basal area over all size classes was significantly higher ($t = 4.0$, $P < 0.01$) in understory sites (4.2 m^2/0.05 ha) than in gaps (2.1 m^2/0.05 ha).

Vegetation profiles showed a marked difference between gaps and forest understory sites during all periods (Fig. 2). We compared distribution of foliage over eight height intervals in gaps and understory sites using ranked abundance of foliage over the eight intervals. Ranked abundances were not correlated between gaps and understory sites during spring or fall.

We distinguished four foliage layers following construction of foliage profiles: ground (0–0.9 m), low canopy (0.9–4.6 m), middle canopy (4.6–9.1 m), and upper canopy (>9.1 m) (Fig. 2). All net sites had dense ground cover, and there was no significant difference in density of ground foliage between gaps and nongaps. Gaps had more vegetation in the low canopy during early ($t = 4.16$, $P < 0.01$), middle (Mann-Whitney test, SND = 2.39, $P < 0.05$), and late ($t = 3.41$, $P < 0.01$) spring periods; understory sites had more vegetation in the upper canopy during all periods (early: $t = 5.04$, $P < 0.001$; middle and late: Mann-Whitney, SND = 2.87, $P < 0.05$ for both periods). Vegetation density in the middle canopy was not significantly different between gaps and forest understory. Gaps had more ground vegetation than understory sites in early fall ($t = 2.40$, $P < 0.05$), but differences between gaps and forest understory sites decreased as ground vegetation declined at all sites from early to late fall (Fig. 2). The distribution of foliage in lower, middle, and upper canopies during fall paralleled spring patterns.

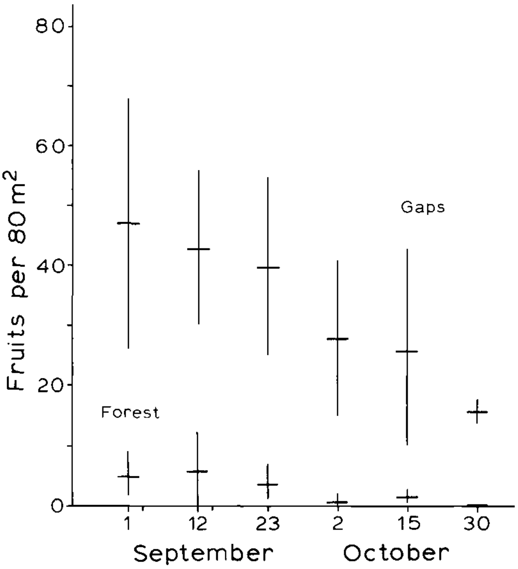

Fig. 3. Abundance of fruits (mean ± 1 SD) at gap and understory sites. Differences between gaps and understory sites were significant on all dates ($t > 6.6$, $P < 0.001$ for all dates).

Fruit and insect abundance.—Abundance of fruit was greater in gaps than in forest understory on all sampling dates in fall ($t > 6.6$, $P < 0.001$ on each sampling date) (Fig. 3). Abundance of ripe fruits was highest early in September and declined thereafter (Fig. 3; gaps: $r = -0.980$, $P < 0.001$; understory: $r = -0.894$, $P < 0.01$; fruit abundance over time). Fruit removal largely was complete in understory sites after the first week in October, but some gaps retained fruit into December (Hoppes unpubl. data). The major source of difference in fruit abundance between gap and understory sites was the absence of fruiting vines such as Virginia creeper, wild grape, and catclaw in forest understory sites. Understory sites either lacked fruit or had only a few fruiting spicebush shrubs.

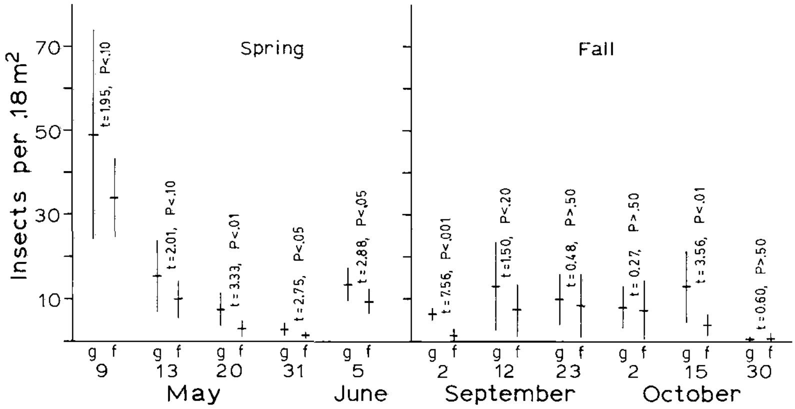

Fig. 4. Number of insects captured (mean ± 1 SD) on sticky traps (4 traps, totaling 0.18 m^2/net site) placed around gap (g) and forest understory (f) nets.

Most insects captured in spring were small (<2 mm) Diptera, although Coleoptera also were well represented. By contrast, most insects captured in fall were large Diptera and Coleoptera, although small Diptera also were common. Average number of captures was higher in gaps during both spring and fall (Fig. 4; Wilcoxon Signed Ranks test, $P < 0.05$ spring and fall). Differences between gaps and understory sites were more pronounced in spring, when significant differences existed on 3 of 5 sampling dates, than in fall, when significant differences existed on only 2 of 6 dates (Fig. 4).

Species numbers and captures of birds.—We captured 1,010 birds (including 69 recaptures, 6.8%), representing 74 species, during 1,416 mist-net hours (1 MNH = 1 mist net open 1 h) in spring, for an overall capture rate of 71 captures/100 MNH. In fall we caught 458 birds (14 recaptures, 3.1%), representing 44 species, during 1,504 MNH, for a capture rate of 31/100 MNH. Capture rates at individual nets ranged from 7 to 161 birds/100 MNH in spring and from 2 to 152 birds/100 MNH in fall. Only two individuals, both in spring, were recaptured on the same day and at the same net. Thus, inclusion of recaptures does not bias results by introducing overrepresentation of individual preferences. All species with number of captures in gap and forest understory nets are listed in the Appendix.

Gap-understory comparisons.—Number of captures was higher in gap than in understory nets on 16 of 18 dates in spring and 20 of 24 dates in fall. Total number of captures and average number of captures per net were higher in gaps than in understory nets during both spring and fall (Table 1). Similarly, average number of species captured per net was higher in gap nets (Table 1). In both seasons, however, the total number of species captured in all gap nets was not significantly greater than the number captured in all understory nets (Table 2), indicating that a lower similarity in species composition existed among forest understory sites than among gaps.

TABLE 1. Captures in gap and forest understory nets during spring (S) and fall (F).

		Gap	Forest	Test	*P*
Total captures	(S)	628	382	$\chi^2 = 60.0$	<0.001
	(F)	356	102	$\chi^2 = 143.0$	<0.001
Captures/net	(S)	105	64	$t = 7.1$	<0.001
	(F)	58	17	$t = 5.9$	<0.001
Total species	(S)	69	60	$\chi^2 = 0.004$	>0.50
	(F)	43	28	$\chi^2 = 3.2$	<0.10
Species/net	(S)	38	27	$t = 9.1$	<0.001
	(F)	20	8	$t = 5.9$	<0.001

TABLE 2. Species with marked differences ($P < 0.01$) in capture frequency between gap and forest understory nets in Trelease Woods, spring and fall 1983.

	Spring			Fall		
	Captures			Captures		
Species[a]	Gap	Forest	P	Gap	Forest	P
Yellow-bellied Flycatcher	20	4	<0.001			
Least Flycatcher	18	9	<0.070			
White-breasted Nuthatch	0	5	<0.062			
Golden-crowned Kinglet				48	7	<0.001
Ruby-crowned Kinglet	10	2	<0.032	21	1	<0.001
Gray-cheeked Thrush	14	6	<0.074			
Swainson's Thrush	49	31	<0.024	13	4	<0.037
Wood Thrush	8	20	<0.023			
Gray Catbird	30	9	<0.001			
Red-eyed Vireo				10	0	<0.002
Magnolia Warbler	22	9	<0.018	22	2	<0.001
Yellow-rumped Warbler	8	17	<0.064			
Blackburnian Warbler				25	5	<0.001
Palm Warbler	0	7	<0.015			
American Redstart	40	5	<0.001	7	0	<0.015
Ovenbird				76	22	<0.001
Northern Waterthrush	23	2	<0.001			
Canada Warbler	16	4	<0.005	7	1	<0.032
White-throated Sparrow	19	9	<0.051			
American Goldfinch	6	0	<0.031			

[a] Scientific names are given in the Appendix.

A minimum of 6 captures is required to attain significance at the 5% level (Fisher Exact Test, 2-tailed). During spring, 44 species had 6 or more captures, and we expected 2.2 species to show a significant difference ($P < 0.05$) in captures between gaps and understory nets based on chance alone. In this study, 11 species displayed a difference in capture frequency at the 5% level and 16 at the 10% level (Table 2), significantly more than expected by chance alone. Two species, Wood Thrush (*Hylocichla mustelina*) and Palm Warbler (*Dendroica palmarum*), were captured significantly more often in forest understory than in gap sites (Table 2). Two other species, White-breasted Nuthatch (*Sitta carolinensis*) and Yellow-rumped Warbler (*Dendroica coronata*), also were captured more often in understory nets, but differences were not significant. The thrush and nuthatch nest in Trelease Woods, and territories are located within undisturbed forest (JGB pers. obs.), accounting for the greater number of captures in forest understory sites. Also, the nuthatch preferentially forages on large trees (JGB pers. obs.), which are uncommon in gaps. Both warblers arrived in Trelease Woods before differences in vegetation between gaps and forest understory sites were apparent. The remaining 12 of the 16 species (Table 2) were caught more often in gap nets.

Species captured significantly more often in gaps were not simply canopy species following the edge of vegetation downward. In fact, most species that showed a preference for gaps (Table 2) were birds of the ground or lower vegetation levels. When all species (including those represented by 1–5 captures) were considered, 51 species were captured more often in gaps and 16 in forest understory nets, a ratio significantly different from even ($\chi^2 = 18.3$, $P < 0.001$). In addition, although 14 species were captured only in gap nets, only 5 were restricted to forest understory ($\chi^2 = 4.26$, $P < 0.05$).

Seventeen species were represented by at least 6 captures in fall, and based on chance alone we expected 1 species to show a significant ($P < 0.05$) difference in number of captures between gaps and understory sites. However, 9 species displayed significant differences in capture frequency between gaps and understory sites (Table 2), and all were captured more frequently in gaps. Only 2 species, White-breasted and Red-breasted nuthatches (*Sitta canadensis*), were captured more frequently in forest understory than in gaps (see Appendix). Thirty-seven species were captured more often

TABLE 3. Captures by trophic groups, in gap and forest understory nets during spring (S) and fall (F). Numbers of captures of species that are frugivorous in fall are shown as a group and subdivided into primary and secondary subgroups.[a]

Trophic group	Season	Species[b]	Captures		χ^2	P
			Gap	Forest		
Flycatchers	S	8.5	80	22	33.0	<0.001
	F	5	9	4	1.9	<0.50
Bark foragers	S	8.5	24	26	0.1	>0.50
	F	4	10	7	0.5	>0.50
Ground insectivores	S	12	204	137	13.2	<0.001
	F	2	79	24	29.4	<0.001
Foliage insectivores	S	33	194	105	26.5	<0.001
	F	16	165	35	89.4	<0.001
Granivore-omnivores	S	11	119	90	4.0	<0.05
	F	5	23	9	6.1	<0.025
Frugivores (total)	S	16	180	129	8.4	<0.005
	F	10	66	23	20.8	<0.001
Primary	S	9	146	92	12.3	<0.001
	F	8	48	17	69.1	<0.001
Secondary	S	7	34	37	0.1	>0.50
	F	2	18	6	6.0	<0.025

[a] Frugivores include species that regularly consume fruit during fall migration. Primary frugivores include: Northern Flicker, thrushes (6 species), Gray Catbird, and Brown Thrasher. Secondary frugivores include: Red-bellied and Red-headed woodpeckers, European Starling, Red-eyed Vireo, Yellow-rumped Warbler, Scarlet Tanager, and Northern Oriole.

[b] Several species were assigned to two groups equally (see Appendix).

in gaps and only 2 in understory sites ($\chi^2 = 31.4$, $P < 0.001$), when all species were considered. Sixteen species were captured only in gaps, while 1 was captured only in forest sites ($\chi^2 = 13.2$, $P < 0.001$).

The distribution of captures among five major trophic groups during spring differed between gap and forest sites ($\chi^2 = 20.8$, 4 df, $P < 0.001$). Bark foragers displayed no difference in frequency of captures between gap and forest nets (Table 3). Other groups, particularly flycatchers, foliage insectivores, and ground insectivores, were caught significantly more often in gap nets (Table 3). Species that are frugivorous in fall were captured more often in gaps during spring (Table 3). When separated into primary and secondary frugivores, primary frugivores preferred gaps, but secondary frugivores displayed no difference in captures between gaps and forest understory (Table 3).

The number of individuals captured in all major trophic groups was higher in gaps than in forest sites during fall (Table 3). Unlike spring, however, the distribution of captures among major trophic groups did not differ between gaps and forest ($\chi^2 = 7.98$, 5 df, $P > 0.05$). Ground insectivores, foliage insectivores, and primary and total frugivores were captured significantly more often in gaps (Table 3).

Vegetation, resource abundance, and number of captures of birds.—Foliage density in the ground and middle canopy layers varied little among sites, and no consistent difference existed between gap and forest sites. Consequently, we examined correlations between capture rates and foliage density in lower- and upper-canopy layers only, using each net as a single sample point ($n = 12$).

During spring, species richness and total number of captures correlated positively with density of vegetation in the lower layer and negatively with density of upper-canopy foliage (Table 4). Similar patterns were evident for number of captures of flycatchers, foliage insectivores, and primary frugivores. Ground insectivores showed no correlation with low-level foliage but correlated negatively with upper-canopy foliage (Table 4).

We compared total number of captures during early, middle, and late spring migration with foliage densities in lower- and upper-canopies during these periods. Number of captures per net correlated positively with foliage in low strata during early (Spearman $r_s = 0.684$,

TABLE 4. Correlations between number of captures and foliage density in lower and upper canopies (LC, UC), insect abundance (IN), and fruit abundance (FR) at gap and forest understory nets. Only significant correlations (Spearman's r) are shown: $P < 0.05$, $r > 0.587$; $P < 0.01$, $r > 0.727$; and $P < 0.001$, $r > 0.846$. See Table 3 for description of frugivore categories.

	Spring			Fall			
	LC	UC	IN	LC	UC	IN	FR
Total species	0.63	−0.81	0.62	0.65	−0.73		0.64
Total captures	0.61	−0.84	0.60	0.72	−0.64		0.63
Flycatchers	0.80	−0.88	0.76		−0.63		
Ground insectivores		−0.61		0.71	−0.73	0.72	0.59
Foliage insectivores	0.67	−0.81	0.74	0.68	−0.73	0.59	
Granivore-omnivores			0.62				
Frugivores (total)					−0.66		0.68
Frugivores (primary)	0.70	−0.89	0.67		−0.69		0.58

$P < 0.05$), middle ($r_s = 0.542$, $P < 0.10$), and late periods ($r_s = 0.684$, $P < 0.05$) and correlated negatively with foliage density in the upper canopy (early, $r_s = -0.474$, $P < 0.20$; middle, $r_s = -0.734$, $P < 0.01$; late, $r_s = -0.787$, $P < 0.01$).

When all net sites were included, only number of foliage insectivores correlated significantly with insect abundance ($r_s = 0.614$, $P < 0.05$). However, number of insects captured at one gap site was significantly less ($t = 2.2$, $P < 0.05$) than the mean for other gap sites. The reasons for the unusually low number of insect captures at one gap are not clear, but the positions of the insect traps or other factors unrelated to actual insect abundance in the gap (e.g. microclimatic conditions) may have unduly influenced the effectiveness of the traps. As a consequence, we reexamined correlations between bird community variables and insect abundance at the remaining 11 sites (see Discussion). Both species richness and number of captures correlated significantly with insect abundance (Table 4). Among trophic groups, flycatchers, in particular, showed a strong correlation with insect abundance (Table 4). When all sites were included, correlations were similar in direction but were not as strong as when the one site was eliminated.

Fall patterns were similar to spring with respect to correlations between number of species and captures and measures of habitat structure (Table 4). Two trophic groups, ground insectivores and foliage insectivores, correlated with foliage density in the lower layer, while 5 groups correlated negatively with upper-canopy foliage (Table 4). Unlike spring, number of captures of all frugivores combined correlated negatively with upper-canopy foliage.

The number of captures per net during early, middle, and late fall migration correlated positively with foliage density in the lower level (early, $r_s = 0.64$, $P < 0.05$; middle, $r_s = 0.56$, $P < 0.10$; late, $r_s = 0.49$, $P < 0.20$). The number of captures correlated negatively with foliage density in the upper level (early, $r_s = -0.45$, $P < 0.20$; middle, $r_s = -0.70$, $P < 0.05$; late, $r_s = -0.70$, $P < 0.05$). The number of captures of only 2 trophic groups, ground insectivores and foliage insectivores, correlated positively with number of insects captured at each net site. Several groups, however, correlated positively with fruit abundance per net (Table 4). When frugivores were separated into primary and secondary groups, only primary frugivores showed a significant association with fruit abundance.

DISCUSSION

Tree-fall gaps represent a distinct microhabitat that differs from the understory of surrounding forest in vegetation structure (e.g. foliage density, tree size distributions), plant species composition, microclimatic conditions, and resource abundance (Geiger 1950, Denslow 1980, Schemske and Brokaw 1981, Brokaw 1982, Chazdon and Fetcher 1984, Martin and Karr 1986). Recent studies (e.g. Karr and Freemark 1983) have demonstrated that birds may select habitats based on slight differences in vegetation or microclimate and thus there is reason to believe that birds are capable of recognizing and selecting tree-fall gaps as a distinct microhabitat in which to forage (Martin and Karr 1986).

Microclimatic conditions within a gap are a function of gap size (in relation to canopy height), shape, orientation, and vegetation structure, particularly with respect to how these factors determine the daily duration of direct insolation (Geiger 1950, Lee 1978, Chazdon and Fetcher 1984). Amount of light, highest daily temperatures, and amount of precipitation reaching the ground are higher in gaps than in adjacent forest understory and also differ within different sections of a gap (Geiger 1950, Denslow 1980, Chazdon and Fetcher 1984). By contrast, relative humidity is lower in gaps than in forest understory (Denslow 1980). Differences in microclimate between gaps and forest understory are particularly pronounced close to the ground, within the range of vegetation sampled by mist nets, and are influenced strongly by vegetation structure. Soil temperatures and temperatures close to the ground generally increase with gap size (Geiger 1950, Schulz 1960 *in* Denslow 1980, Denslow 1980).

Differences in amount of radiation penetrating to the forest floor in tree-fall gaps and undisturbed forest vary with season and gap age, and may change over time within a season (Geiger 1950, Chazdon and Fetcher 1984). In temperate deciduous forests, the amount of light reaching the forest floor early in spring is only slightly greater in gaps than in forest understory. As the canopy closes with continued leaf production, however, the difference in amount of radiation penetrating below the canopy in gaps and undisturbed forest increases (Anderson 1964).

Birds that use lower levels of a forest may be attracted to gaps because of a greater abundance of resources or because resources may be more accessible or visible in gaps (i.e. because of higher light levels) than in forest understory (Schemske and Brokaw 1981, Willson et al. 1982). During spring, most birds feed on insects and other invertebrates, and several lines of evidence suggest that such resources are more abundant or concentrated in gaps than in forest understory.

Lepidopteran larvae form a major component of the diet of many foliage-gleaning species, and warbler migration in spring coincides with the peak emergence of larvae (Graber and Graber 1983). Tree-fall gaps support relatively dense foliage in low levels, much of it produced by pioneer or early successional species. Plant species are not equally palatable to generalist herbivores, and a continuum of palatability exists from weedy species to gap colonists to mature forest species (Cates and Orians 1975, Hartshorn 1978). Thus, gaps not only support greater concentrations of foliage than similar areas within forest understory but also support relatively higher proportions of foliage that are palatable to a broad variety of herbivorous invertebrates. Although foliage density does not directly measure abundance of foliage insects, it can be taken as an indirect measure of such abundance because foliage density does directly measure availability of feeding substrates for insects and searching substrates for foliage-gleaning birds.

Most insectivorous groups occurred more frequently in gaps in spring and fall, supporting the hypothesis that birds select gaps as profitable foraging locations (Martin and Karr 1986). Correlations between insectivorous groups (e.g. foliage insectivores) and foliage densities provide indirect evidence that a greater resource abundance attracts many species to gaps (Martin and Karr 1986, this study). Furthermore, bark insectivores exhibited little or no preference for gaps in spring or fall and foraging substrates for this group are less abundant in gaps, making gaps less attractive as foraging sites. Schemske and Brokaw (1981) found relatively few species concentrated in gaps in Panamanian forest, but those species considered gap specialists were insectivorous to a great extent.

A greater abundance of foliage and insects reduces the amount of time required for searching and travel and results in a faster rate of food ingestion. This may be particularly important during migration, when energy requirements are high (Graber and Graber 1983). During spring, migrants are moving toward areas where food supplies and weather may be unpredictable. Thus, there may be greater pressure during spring than during fall to select the most profitable sites in which to forage.

Leaf litter often is abundant in gaps, and consequently soil and litter invertebrates are likely to be abundant as well (Bultman and Uetz 1984 and references therein). Higher soil and near-ground temperatures in gaps, relative to forest understory, also may increase insect activity levels over that present in forest understory. If soil invertebrates are more abundant in gaps than in forest understory locations, particularly early in spring, this is a likely explanation for the greater abundance of ground insectivores in gaps over forest understory.

Finally, our study provides direct evidence that flying insects, primarily Diptera and Coleoptera, are more abundant in gaps. Coleoptera form a major component of the diet of many flycatchers in Illinois (Graber et al. 1974), and flycatchers showed a strong correlation with insect abundance during spring. Higher light levels and a greater number of low (under 4.6 m) perches, combined with a greater abundance of insects, may make gaps an especially profitable location for flycatching insectivores. During fall, differences in insect abundance were less pronounced between gaps and forest, and thus it would be less advantageous for flycatchers to concentrate their activities in gaps than in understory sites. Fall migration characteristically is much less pronounced than spring migration (Graber et al. 1974), and the lack of correlation between flycatchers and insect abundance may reflect the low number of flycatchers caught in fall ($n = 13$). Little is known of the habitat preferences of migrants, and migrants may select different habitats (e.g. forest edge) in fall than in spring (e.g. Austin 1970).

Many species in Illinois rely on fruits for a major part of their diet during fall (Martin et al. 1951; Thompson and Willson 1978, 1979), and the availability and diversity of fruits is greater in gaps than in forest understory (Thompson and Willson 1978, 1979). The abundance of fruits in gaps appears to attract many frugivores (Thompson and Willson 1978, Martin and Karr 1986), and our sampling of actual fruit abundance and bird abundance supports this suggestion. Those species most dependent on fruit during fall ("primary frugivores") were more strongly correlated with fruit abundance than were species with a more mixed fruit and insect diet ("secondary frugivores"). The latter species may consume fruits when they are encountered but may not actively search for areas with high fruit concentrations. Total species and total captures per net correlated with insect abundance in spring and with fruit abundance in fall, reflecting the switch in diet of a substantial proportion of birds captured during spring and fall migration.

Birds may select foraging locations on the basis of actual resource levels (e.g. insect abundance) or on the basis of an indirect index of resource abundance (e.g. light levels, foliage density) (Martin and Karr 1986). Fewer insects were captured on sticky traps at one gap than at remaining gaps during spring. The actual cause for the low number is unknown and may represent simple chance events. The gap itself was smaller than the others, and differences in microclimate directly related to gap size may have influenced insect activity levels. Despite the apparently low insect abundance, bird captures were still higher than in forest understory sites and more comparable to other gap sites. It is possible that birds were attracted to the gap because of higher light levels and foliage density, relative to surrounding forest understory, on the expectation that insect abundance would be greater. However, correlation between bird and flying insect abundance was strongest for flycatchers when the one unusual net was eliminated, suggesting assessment of actual abundance. Further, in a comparison of bird use of new and old gaps, Martin and Karr (1986) found evidence to suggest that birds were not simply responding to higher light levels in gaps.

Birds may be attracted to gaps because of increased cover in lower levels, perhaps as protection from predators. If this were the case, we might expect all trophic groups to show a similar response to density of foliage. Only flycatchers and foliage insectivores were correlated with low foliage density in spring, however, and in fall only ground and foliage insectivores were. The positive correlation of foliage insectivores with foliage density and the general lack of correlation exhibited by other groups suggest that availability of cover was not a primary factor influencing distribution patterns of individuals [see Martin and Karr (1986) for further discussion on this point].

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APPENDIX. Number of captures in gap and forest understory nets in Trelease Woods, Illinois, during spring and fall migration, 1983. Species that belong to different trophic groups in spring (S) and fall (F) have groups indicated for both seasons. Nomenclature follows the A.O.U. check-list (1983).

	Captures				
	Gap		Forest		
Species	S	F	S	F	Trophic group
Ruby-throated Hummingbird (*Archilochus colubris*)	7	4	2		Nectarivore
Red-headed Woodpecker (*Melanerpes erythrocephalus*)			2		Bark forager
Red-bellied Woodpecker (*Melanerpes carolinus*)	1		1		Bark forager
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	3		4		Bark forager
Downy Woodpecker (*Picoides pubescens*)	3		4		Bark forager
Hairy Woodpecker (*Picoides villosus*)	2		1		Bark forager
Northern Flicker (*Colaptes auratus*)	4	5	2	1	Ground and bark forager (S), frugivore (F)
Olive-sided Flycatcher (*Contopus borealis*)	4				Flycatcher
Eastern Wood-Pewee (*Contopus virens*)	6	2	1	1	Flycatcher
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	20	2	4		Flycatcher
Acadian Flycatcher (*Empidonax virescens*)	2		1		Flycatcher
Empidonax sp.[a]	2	3		2	Flycatcher
Least Flycatcher (*Empidonax minimus*)	18	1	9	1	Flycatcher
Eastern Phoebe (*Sayornis phoebe*)	1	1	1		Flycatcher
Great Crested Flycatcher (*Myiarchus crinitus*)	7		3		Flycatcher
Blue Jay (*Cyanocitta cristata*)	8	2	5		Omnivore-granivore
Red-breasted Nuthatch (*Sitta canadensis*)		1		2	Bark forager
White-breasted Nuthatch (*Sitta carolinensis*)			5	1	Bark forager
Brown Creeper (*Certhia americana*)	8	3	4		Bark forager
Carolina Wren (*Thryothorus ludovicianus*)		1			Foliage insectivore
Winter Wren (*Troglodytes troglodytes*)	1	3		1	Foliage insectivore
Golden-crowned Kinglet (*Regulus satrapa*)	1	48	2	7	Foliage insectivore
Ruby-crowned Kinglet (*Regulus calendula*)	10	21	2	1	Foliage insectivore
Veery (*Catharus fuscescens*)	12	2	6	1	Ground insectivore (S), frugivore (F)
Gray-cheeked Thrush (*Catharus minimus*)	14	4	6	3	Ground insectivore (S), frugivore (F)
Swainson's Thrush (*Catharus ustulatus*)	49	13	31	4	Ground insectivore (S), frugivore (F)
Hermit Thrush (*Catharus guttatus*)	1	12		6	Ground insectivore (S), frugivore (F)
Wood Thrush (*Hylocichla mustelina*)	8	3	20	1	Ground insectivore (S), frugivore (F)
American Robin (*Turdus migratorius*)	25	6	17	1	Ground insectivore (S), frugivore (F)
Gray Catbird (*Dumetella carolinensis*)	30	3	9		Ground-foliage insectivore (S), frugivore (F)
Brown Thrasher (*Toxostoma rufum*)	3		1		Ground insectivore
European Starling (*Sturnus vulgaris*)	4		5		Ground insectivore
White-eyed Vireo (*Vireo griseus*)	1	2			Foliage insectivore
Solitary Vireo (*Vireo solitarius*)	2				Foliage insectivore
Warbling Vireo (*Vireo gilvus*)	1				Foliage insectivore
Red-eyed Vireo (*Vireo olivaceus*)	10	10	8		Foliage insectivore (S), frugivore (F)
Golden-winged Warbler (*Vermivora chrysoptera*)	2				Foliage insectivore
Tennessee Warbler (*Vermivora peregrina*)	9	1	3		Foliage insectivore

APPENDIX. Continued.

Species	Captures				Trophic group
	Gap		Forest		
	S	F	S	F	
Nashville Warbler (*Vermivora ruficapilla*)	11	4	8		Foliage insectivore
Yellow Warbler (*Dendroica petechia*)			1		Foliage insectivore
Chestnut-sided Warbler (*Dendroica pensylvanica*)	3	1	3		Foliage insectivore
Magnolia Warbler (*Dendroica magnolia*)	22	22	9	2	Foliage insectivore
Black-throated Blue Warbler (*Dendroica caerulescens*)	2				Foliage insectivore
Yellow-rumped Warbler (*Dendroica coronata*)	8	8	17	6	Foliage insectivore (S), frugivore (F)
Black-throated Green Warbler (*Dendroica virens*)	6	1	7	1	Foliage insectivore
Blackburnian Warbler (*Dendroica fusca*)	4	25	2	5	Foliage insectivore
Palm Warbler (*Dendroica palmarum*)			7		Foliage insectivore
Bay-breasted Warbler (*Dendroica castanea*)	9	19	4	16	Foliage insectivore
Blackpoll Warbler (*Dendroica striata*)	1	1	4	1	Foliage insectivore
Black-and-white Warbler (*Mniotilta varia*)	5	6	4	4	Bark forager
American Redstart (*Setophaga ruticilla*)	40	7	5		Flycatcher and foliage insectivore
Worm-eating Warbler (*Helmitheros vermivorus*)	1		1		Foliage insectivore
Ovenbird (*Seiurus aurocapillus*)	47	76	42	22	Ground insectivore
Northern Waterthrush (*Seiurus noveboracensis*)	23	3	2	2	Ground insectivore
Louisiana Waterthrush (*Seiurus motacilla*)	1		1		Ground insectivore
Kentucky Warbler (*Oporornis formosus*)	6		4		Foliage insectivore
Connecticut Warbler (*Oporornis agilis*)	3				Foliage insectivore
Mourning Warbler (*Oporornis philadelphia*)	11		5		Foliage insectivore
Common Yellowthroat (*Geothlypis trichas*)	5	1	2		Foliage insectivore
Hooded Warbler (*Wilsonia citrina*)			1		Foliage insectivore
Wilson's Warbler (*Wilsonia pusilla*)	1	1			Foliage insectivore
Canada Warbler (*Wilsonia canadensis*)	16	7	4	1	Foliage insectivore
Yellow-breasted Chat (*Icteria virens*)	1		1		Foliage insectivore
Scarlet Tanager (*Piranga olivacea*)	7		3		Foliage insectivore
Northern Cardinal (*Cardinalis cardinalis*)	7		2		Omnivore-granivore
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1	5	5		Omnivore-granivore
Indigo Bunting (*Passerina cyanea*)	66		56		Omnivore-granivore
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	3				Omnivore-granivore
Fox Sparrow (*Passerella iliaca*)		1		1	Omnivore-granivore
Lincoln's Sparrow (*Melospiza lincolnii*)			2		Omnivore-granivore
Swamp Sparrow (*Melospiza georgiana*)	1		1		Omnivore-granivore
White-throated Sparrow (*Zonotrichia albicollis*)	19	1	9	1	Omnivore-granivore
Common Grackle (*Quiscalus quiscula*)	1	14	5	7	Omnivore-granivore
Brown-headed Cowbird (*Molothrus ater*)	7		5		Omnivore-granivore
Orchard Oriole (*Icterus spurius*)	1				Foliage insectivore
Northern Oriole (*Icterus galbula*)	4		1		Foliage insectivore
American goldfinch (*Carduelis tristis*)	6				Omnivore-granivore

[a] Probably Willow Flycatcher (*Empidonax traillii*).