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MIGRATION OF WOODLAND BIRDS AT A FRAGMENTED INLAND STOPOVER SITE

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ABSTRACT.—The abundance, timing, and habitat distribution of woodland-associated migrants were examined at a migratory stopover site in the St. Croix River Valley, Washington County, Minnesota during spring and autumn migrations, 1984–1986. Five wooded habitats (1–3+ ha) were studied using mist nets. Migrants made up 92% of the species (N = 100) and 94.8% of the individuals (N = 17,019) captured. Of the 69 most common migrant species, 58 (84%) were Nearctic-Neotropic migrants. Analyses of median passage dates suggest that peak numbers, and thus resource demands, occurred in the days surrounding 14 May and 31 August. Eighteen migrant species (53% of those adequately covered by our study periods) showed a difference between median spring and autumn passage of 105 days or less, and thus spend less than 30% of their annual life cycles on their breeding grounds. Seasonal absences or higher capture rates in spring suggest that seven species in our region use migratory routes differing from the regional norm. The distributions of birds at our site changed between seasons, suggesting a spatial shift in habitat use by the entire avian community. *Received 9 Dec. 1991, accepted 1 April 1992.*

Migratory stopover sites serve as refueling locations for many migrant passerines, especially those that are physically unable to carry enough fuel (fat) to complete an entire season's migration in one migratory episode (probably most Nearctic-Neotropic passerine migrants; see Berthold 1975; Dawson et al. 1983; Bairlein 1987; Winker et al., in press). Despite the probable importance of stopover sites in the annual life cycles of passerine migrants, very little is known about the demand placed upon the resources at these sites. This ignorance is extensive, existing at local, regional, and continental levels. Broad questions regarding Nearctic-Neotropic passerine migration (e.g., route selection and habitat preferences) remain unanswered. This confounds efforts to understand evolutionary questions regarding these species and may thwart the development of effective conservation policies for migrant populations showing declines (see Robbins et al. 1989, Terborgh 1989).

We believe that a comprehensive picture of Nearctic passerine migration is needed and that many of the data to construct this picture can be obtained only through geographically widespread, multi-year, multi-habitat, single-site banding efforts. Site-specific summary statistics would be very useful in illuminating broad, species-specific aspects of route selection, timing, and habitat preferences. Those data of particular importance in this regard are relative "densities" of birds occurring at a site, structure

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TABLE 1

SEASONAL AND ANNUAL DISTRIBUTIONS OF SAMPLE EFFORT (NET-H)

Year	Net-h-1	
	Spring	Autumn
1984	17,708	22,971
1985	26,667	24,999
1986	27,023	17,829
Total	71,398	65,799

of habitats sampled, some idea of what portion of the migration period was covered by the sample effort, and the median date of individual passage. In this paper we summarize migration at a site in eastern Minnesota and examine our data from local and regional levels.

STUDY AREA AND METHODS

Our study site was located approximately 2 km from the St. Croix River, near Afton, Washington County, Minnesota (44°55'N 92°48'W), in a mosaic of suburban-residential, agricultural, and wooded tracts. Unlike many studies of Nearctic migrants (see refs. in Winker et al. 1992), this site was located far from any ecological barrier to migration (e.g., large body of water, mountains, desert). Our sampling program included five relatively discrete wooded habitat patches which ranged in size from approximately 1–3+ ha. These habitats, representative of the area's native woodlands, were called Floodplain, Swamp, Upland, Willows, and Oaks. Upland and Oaks were well-drained sites; Swamp, Floodplain, and Willows were moister (with occasional shallow pools of surface water) and were close to Valley Creek, a small stream flowing through the site.

Standard mist nets (12 m × 2.6 m of 30- and 36-mm mesh) were placed 30 m apart along lines that were themselves 30 m apart. The ends of the nets were pointed E and W, enabling the capture of birds moving N or S. The number of nets in each habitat varied according to patch size: Floodplain (18), Swamp (12), Upland (18), Willows (12), and Oaks (10). Nocturnal captures were rare, and nets were closed only for inclement weather or personnel limitations. Sample effort (mist net hours, or net-h) was recorded daily; on days when nets were not closed, net-h were calculated as sunrise-to-sunset time plus 0.5 h. The specific net of capture was among the data recorded for every captured bird. Nets were operated 1–27 May and 9 Aug.–24 Sept. 1984, 29 Apr.–29 May and 14 Aug.–22 Sept. 1985, and 28 Apr.–28 May and 17 Aug.–23 Sept. 1986. Thus, our overall sample effort spanned 32 days in spring (Julian days 118–149) and 47 days in autumn (Julian days 222–268). The distribution of sample effort varied seasonally and annually (Table 1). Analyses of habitat distribution employ data from days on which the habitats considered were sampled simultaneously (see Winker et al., in press, for more details).

The vegetative structure and composition of each habitat (Appendix) was measured using the method of James and Shugart (1970) with slight modifications. We centered our examinations on the center of each net lane, measuring the vegetation in two semicircles (11.35 m radius) separated by 2 m (total area 0.04 ha). This effectively removed the bare, 1.5–2 m net lane from consideration. We also used a range-finder for increased accuracy in determining the limits of the 11.35 m radius. Shrub taxa were included, and we present those which comprised 90% of the total shrub stem count. All net locations were sampled, thus our minimum sample in any habitat was ten 0.04-ha circles (Oaks), which is twice the minimum number recommended by James and Shugart (1970). Because nets were placed on a 30 m grid, we consider that tree analysis directly measured approximately 50% of the area our nets were placed to sample, and that shrub analysis directly measured approximately 5% of the same area.

RESULTS

During six seasons of netting we captured 17,019 birds of 100 species. These figures alone suggest substantial use of these small wooded patches by transient migrants. Evidence considered elsewhere suggests that migrants at our site were feeding—some on an impressive scale (Winker et al., in press, unpubl. data). Resources at this site were used by migrants for fattening in spring and for fattening and molting in autumn (molt occurred among transient as well as locally breeding species; Winker et al. 1991, in press, unpubl. data). When examined on a seasonal basis, capture rates varied considerably among years (Table 2). Much of this variation was no doubt due to weather variability. Eight of the 100 species encountered at our site during migration were permanent residents, and these species made up 5.2% of the total individuals captured. Of the 92 species of migrants, 69 species were represented by 10 or more individuals (Table 2). Of these 69 migrant species 58 (84%) were Nearctic-Neotropic migrants (after Rappole et al. 1983:108).

Timing.—Our netting periods spanned the bulk of both spring and autumn migration (Fig. 1), but did not encompass the full migratory periods of several species, most of which were Nearctic-Neotropic migrants (unpubl.). An examination of individual passage through time (Fig. 1, unpubl.) reveals that the largest numbers of birds occurred at our site near the middle of our netting periods. Analyses of median passage times suggest that peak resource demands (as reflected in numbers of birds present) occurred in the days surrounding 14 May (Julian day 134) and 31 Aug. (Julian day 243) which are the median dates of passage for the combination of all individuals of migrant species in Table 2.

Elsewhere (Winker et al., in press), we found that the availability of median date information in the literature allowed us to examine the speed of northward passage in Swainson's Thrush in spring. Although spring passage has received much attention, autumn passage data are largely nonexistent for most migrant species. Here we present both spring and autumn median passage data for many of the migrants at our site (Table 2), hoping that others will find them useful for making geographic comparisons. Four species showed a difference between spring and autumn median passage at our site of 95 days or less: the Yellow-bellied Flycatcher,

TABLE 2

SUMMARY OF CAPTURES BY SEASON (1984–1986) FOR SPECIES REPRESENTED BY MORE THAN 10 INDIVIDUALS. RECAPTURES ARE EXCLUDED. RESIDENT SPECIES ARE INCLUDED TO PORTRAY LOCAL COMMUNITY STRUCTURE AND TO ALLOW RELATIVE ABUNDANCE ESTIMATES. MEDIAN DATES OF OCCURRENCE ARE NOT GIVEN FOR RESIDENT SPECIES, NOR FOR MIGRANT SPECIES WHOSE SEASONAL MOVEMENTS WERE NOT ADEQUATELY ENCOMPASSED BY OUR SAMPLE PERIODS

		SPRING[a]				AUTUMN[b]			
Species	Status[c]	N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
American Woodcock (*Scolopax minor*)	M	8	121–147	—	0.11 (0.06–0.16)	6	233–264	—	0.09 (0.06–0.12)
Ruby-throated Hummingbird (*Archilochus colubris*)	M	86	128–148	140	1.22 (0.34–2.26)	387	227–265	241	5.88 (5.05–7.04)
Red-bellied Woodpecker (*Melanerpes carolinus*)	R	5	122–135	—	0.07 (0.04–0.11)	7	234–267	—	0.11 (0.06–0.16)
Downy Woodpecker (*Picoides pubescens*)	R	45	118–148	—	0.64 (0.30–1.58)	105	226–266	—	1.60 (1.18–1.88)
Hairy Woodpecker (*P. villosus*)	R	21	121–135	—	0.30 (0.04–0.73)	30	227–262	—	0.46 (0.30–0.60)
Yellow-shafted Flicker (*Colaptes a. auratus*)	M	2	132–142	—	0.03 (0.00–0.06)	8	231–264	—	0.12 (0.04–0.22)
Olive-sided Flycatcher (*Contopus borealis*)	T	2	135–140	—	0.03 (0.00–0.06)	52	229–251	241	0.81 (0.64–1.23)
Eastern Wood-Pewee (*C. virens*)	M	8	137–147	142–3	0.11 (0.00–0.34)	97	229–264	243	1.47 (1.23–1.68)
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	T	28	138–148	146	0.40 (0.11–0.96)	236	229–264	240	3.59 (1.74–4.66)
"Traill's" Flycatcher (*E. "traillii"* spp.)	T	41	125–149	143	0.67 (0.37–1.52)	207	229–264	240	3.15 (2.00–4.21)
Least Flycatcher (*E. minimus*)	T	326	118–148	133	4.36 (1.11–13.78)	153	229–265	242	2.33 (1.39–3.16)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a] N	SPRING[a] Date range[d]	SPRING[a] Median	SPRING[a] Mean birds/1000 net-h (Range)[e]	AUTUMN[b] N	AUTUMN[b] Date range[d]	AUTUMN[b] Median	AUTUMN[b] Mean birds/1000 net-h (Range)[e]
Eastern Phoebe (*Sayornis phoebe*)	M	4	119–138	—	0.06 (0.00–0.12)	21	232–266	247	0.32 (0.17–0.45)
Great Crested Flycatcher (*Myiarchus crinitus*)	M	14	127–147	140	0.20 (0.00–0.51)	34	227–262	235–6	0.52 (0.13–0.80)
Blue Jay (*Cyanocitta cristata*)	R	24	121–147	—	0.34 (0.19–0.62)	31	230–267	—	0.47 (0.26–0.80)
Black-capped Chickadee (*Parus atricapillus*)	R	134	118–147	—	1.90 (1.01–4.12)	325	222–267	—	4.94 (4.22–5.84)
Red-breasted Nuthatch (*Sitta canadensis*)	T	7	119–138	—	0.10 (0.04–0.28)	35	235–265	—	0.53 (0.00–1.40)
White-breasted Nuthatch (*S. carolinensis*)	R	35	120–147	—	0.50 (0.23–1.19)	42	226–265	—	0.64 (0.45–0.88)
Brown Creeper (*Certhia americana*)	T	9	122–134	—	0.13 (0.00–0.51)	27	242–267	—	0.41 (0.30–0.48)
House Wren (*Troglodytes aedon*)	M	95	118–148	—	1.35 (1.15–1.58)	105	226–266	238	1.60 (0.56–2.32)
Winter Wren (*T. troglodytes*)	T	3	118–123	—	0.04 (0.00–0.11)	40	248–267	—	0.62 (0.56–0.68)
Golden-crowned Kinglet (*Regulus satrapa*)	T	0	—	—	— —	10	255–265	—	0.15 (0.00–0.32)
Ruby-crowned Kinglet (*R. calendula*)	T	241	118–139	—	3.42 (0.78–8.30)	97	243–267	—	1.47 (1.24–1.85)
Blue-gray Gnatcatcher (*Polioptila caerulea*)	M	10	118–147	134–5	0.14 (0.00–0.23)	6	229–244	—	0.09 (0.00–0.20)
Veery (*Catharus fuscescens*)	T	45	120–146	136	0.64 (0.37–1.41)	67	229–267	243	1.02 (0.26–1.51)
Gray-cheeked Thrush (*C. minimus*)	T	149	124–148	132	2.11 (0.93–5.14)	48	238–265	256-7	0.73 (0.30–1.16)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a] N	SPRING[a] Date range[d]	SPRING[a] Median	SPRING[a] Mean birds/1000 net-h (Range)[e]	AUTUMN[b] N	AUTUMN[b] Date range[d]	AUTUMN[b] Median	AUTUMN[b] Mean birds/1000 net-h (Range)[e]
Swainson's Thrush (*C. ustulatus*)	T	347	119–148	138	4.91 (1.81–12.65)	663	229–267	254	10.08 (5.01–14.36)
Hermit Thrush (*C. guttatus*)	T	12	119–137	—	0.17 (0.04–0.34)	3	232–264	—	0.05 (0.00–0.08)
Wood Thrush (*Hylocichla mustelina*)	M	43	125–147	139	0.61 (0.30–1.41)	31	231–266	251	0.47 (0.11–0.83)
American Robin (*Turdus migratorius*)	M	38	118–147	—	0.54 (0.35–0.70)	53	229–266	—	0.81 (0.60–1.13)
Gray Catbird (*Dumetella carolinensis*)	M	233	125–148	139	3.31 (2.60–5.99)	401	222–267	—	6.11 (5.72–6.44)
Cedar Waxwing (*Bombycilla cedrorum*)	M	291	119–148	—	4.13 (0.97–7.51)	136	229–266	—	2.07 (1.61–3.25)
Solitary Vireo (*Vireo solitarius*)	T	99	122–145	133	1.41 (0.04–5.31)	137	233–267	255	2.08 (1.96–2.19)
Yellow-throated Vireo (*V. flavifrons*)	T	0	—	—	— —	13	230–266	242	0.20 (0.04–0.32)
Warbling Vireo (*V. gilvus*)	T	10	127–146	140	0.14 (0.00–0.51)	12	235–263	244	0.18 (0.11–0.26)
Philadelphia Vireo (*V. philadelphicus*)	T	11	127–145	135	0.16 (0.04–0.40)	166	230–266	249	2.52 (2.05–3.65)
Red-eyed Vireo (*V. olivaceus*)	M	37	130–148	142	0.53 (0.19–1.47)	745	229–267	243	11.32 (4.96–15.52)
Blue-winged Warbler (*Vermivora pinus*)	M	24	127–146	134-5	0.34 (0.19–0.73)	8	229–250	236	0.12 (0.11–0.13)
Golden-winged Warbler (*V. chrysoptera*)	T	12	127–140	135	0.17 (0.07–0.34)	46	234–263	244	0.70 (0.56–0.90)
Tennessee Warbler (*V. peregrina*)	T	38	127–144	134	0.54 (0.31–0.68)	777	226–266	240	11.81 (3.48–18.88)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a]				AUTUMN[b]			
		N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
Orange-crowned Warbler (*V. celata*)	T	48	118–135	—	0.68 (0.51–1.07)	11	251–266	—	0.18 (0.04–0.35)
Nashville Warbler (*V. ruficapilla*)	T	143	120–147	134	2.03 (0.89–3.84)	715	229–267	248	10.93 (9.84–12.16)
Northern Parula (*Parula americana*)	T	0	—	—	— —	13	239–253	249	0.20 (0.08–0.35)
Yellow Warbler (*Dendroica petechia*)	T	26	124–147	135	0.37 (0.07–0.96)	3	230–244	—	0.05 (0.00–0.08)
Chestnut-sided Warbler (*D. pensylvanica*)	T	31	130–147	138	0.44 (0.30–0.56)	386	229–267	242	5.87 (3.70–8.76)
Magnolia Warbler (*D. magnolia*)	T	105	126–149	137	1.49 (0.70–3.73)	778	229–267	242	11.84 (5.53–18.40)
Cape May Warbler (*D. tigrina*)	T	0	—	—	— —	47	229–262	238	0.71 (0.00–1.20)
Black-throated Blue Warbler (*D. caerulescens*)	T	0	—	—	— —	11	240–261	252	0.17 (0.13–0.22)
Myrtle Warbler (*D. c. coronata*)	T	84	118–135	—	1.19 (0.19–2.94)	15	229–266	—	0.23 (0.08–0.45)
Black-throated Green Warbler (*D. virens*)	T	7	132–137	135	0.10 (0.00–0.28)	82	233–264	244	1.25 (1.16–1.40)
Blackburnian Warbler (*D. fusca*)	T	3	135–145	—	0.04 (0.00–0.11)	57	229–265	242	0.87 (0.44–1.44)
Western Palm Warbler (*D. p. palmarum*)	T	15	118–133	—	0.21 (0.12–0.30)	3	250–263	—	0.05 (0.00–0.12)
Bay-breasted Warbler (*D. castanea*)	T	0	—	—	— —	184	229–266	245	2.80 (1.52–3.93)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a]				AUTUMN[b]			
		N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
Blackpoll Warbler (*D. striata*)	T	8	135–138	136-7	0.11 (0.00–0.45)	7	249–261	255	0.11 (0.00–0.39)
Black-and-white Warbler (*Mniotilta varia*)	T	84	125–146	133	1.19 (0.07–4.01)	275	226–265	242	4.19 (1.78–6.64)
American Redstart (*Setophaga ruticilla*)	T	94	125–148	139-40	1.33 (0.52–3.11)	527	229–267	242	8.01 (5.49–11.36)
Ovenbird (*Seiurus aurocapillus*)	M	165	120–148	135	2.34 (1.63–4.35)	658	229–267	247	10.03 (6.79–13.76)
Northern Waterthrush (*S. noveboracensis*)	T	431	118–148	132	6.12 (3.48–9.88)	234	227–265	245	3.57 (3.35–4.04)
Connecticut Warbler (*Oporornis agilis*)	T	4	141–146	–	0.06 (0.00–0.17)	47	230–263	243	0.71 (0.44–1.00)
Mourning Warbler (*O. philadelphia*)	T	88	135–148	142-3	1.25 (0.67–2.03)	124	230–264	242	1.88 (1.26–2.84)
Common Yellowthroat (*Geothlypis trichas*)	M	245	121–148	139	3.48 (2.00–6.55)	217	222–267	242	3.30 (2.64–4.09)
Wilson's Warbler (*Wilsonia pusilla*)	T	119	126–147	138	1.69 (0.41–4.57)	158	229–264	243	2.40 (1.35–3.28)
Canada Warbler (*W. canadensis*)	T	45	124–148	145	0.64 (0.37–1.07)	222	229–266	240	3.37 (1.92–4.16)
Scarlet Tanager (*Piranga olivacea*)	M	17	134–148	140	0.24 (0.00–0.79)	21	233–267	245	0.35 (0.00–0.57)
Northern Cardinal (*Cardinalis cardinalis*)	R	59	118–148	–	0.84 (0.81–0.90)	23	230–264	–	0.35 (0.17–0.44)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	M	83	125–148	135	1.18 (0.70–2.43)	261	226–267	244	3.98 (3.81–4.09)

TABLE 2
CONTINUED

		SPRING[a]				AUTUMN[b]			
Species	Status[c]	N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
Indigo Bunting (*Passerina cyanea*)	M	72	125–149	142	1.02 (0.78–1.40)	43	226–265	236	0.65 (0.06–1.35)
Chipping Sparrow (*Spizella passerina*)	M	32	121–149	—	0.45 (0.15–1.02)	3	237–249	—	0.05 (0.00–0.12)
Field Sparrow (*S. pusilla*)	M	5	121–141	—	0.07 (0.06–0.08)	10	235–267	—	0.15 (0.00–0.39)
Song Sparrow (*Melospiza melodia*)	M	58	118–148	—	0.82 (0.79–0.86)	122	222–264	—	1.85 (1.40–2.13)
Lincoln's Sparrow (*M. lincolnii*)	T	32	122–146	131-2	0.45 (0.11–0.90)	15	250–267	—	0.26 (0.00–0.57)
Swamp Sparrow (*M. georgiana*)	T	138	118–145	126	1.96 (0.89–4.91)	13	250–265	—	0.20 (0.00–0.56)
White-throated Sparrow (*Zonotrichia albicollis*)	T	224	118–141	—	3.18 (1.59–6.32)	155	229–267	—	2.40 (1.48–3.87)
Brown-headed Cowbird (*Molothrus ater*)	M	12	127–148	—	0.17 (0.08–0.34)	0	—	—	— —
Baltimore Oriole (*Icterus g. galbula*)	M	22	133–149	140-1	0.31 (0.11–0.90)	20	230–244	237	0.30 (0.00–0.48)
Purple Finch (*Carpodacus purpureus*)	T	3	122–128	—	0.04 (0.00–0.07)	203	231–264	—	3.09 (0.26–4.68)
Pine Siskin (*Carduelis pinus*)	M	21	119–145	—	0.30 (0.04–0.79)	9	249–259	—	0.14 (0.00–0.50)
American Goldfinch (*C. tristis*)	M	132	121–148	—	1.87 (1.30–2.76)	686	226–267	—	10.43 (2.75–24.47)

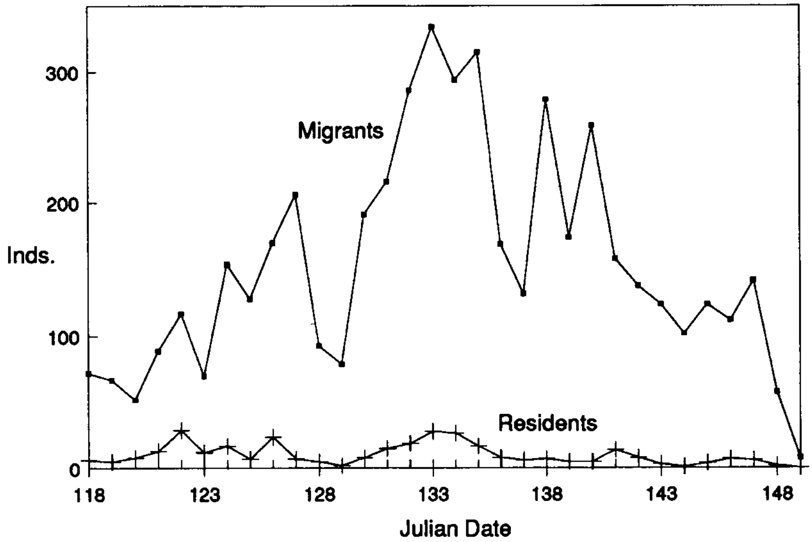
[a] Includes days 118–149.

[b] Includes days 222–268.

[c] Species' status at our site. M = migrant species with resident breeding populations; R = resident species; T = transient species (in some cases the species is known to breed in the region, but our site did not have a breeding population).

[d] Earliest and latest Julian dates of capture within the particular season.

[e] Average capture rates over all three years expressed as birds per 1000 net-h. "Range" shows minimum and maximum annual rates.



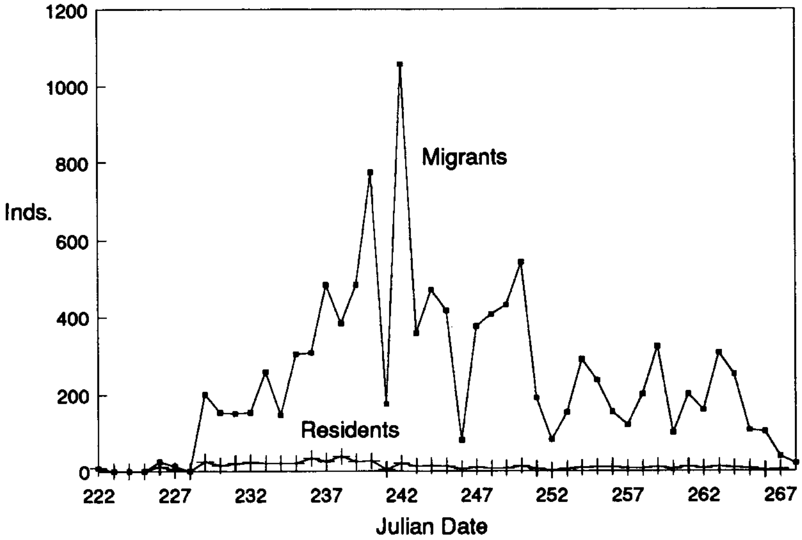


FIG. 1. Total number of birds captured by Julian day during spring (top) and autumn (bottom), 1984–1986. In non-leap years, 15 May = Day 135 and 1 September = Day 244.

Least Flycatcher, Canada Warbler, and Indigo Bunting (scientific names in Table 2). Three-quarters or more of the annual life cycles of the populations of these species that we sampled are thus spent away from the breeding grounds. The Yellow-bellied and Least flycatchers have been shown elsewhere to spend very little time on their breeding grounds; in both species the adults undergo flight feather molt on the wintering grounds following autumn migration (Hussell 1981, 1982). Eighteen of the migrant species in Table 2 showed a difference between median spring and autumn passage of 105 days or less (counting the *Empidonax "traillii"* complex as one species). Thus, about 53% of those migrant species whose seasonal movements were adequately encompassed by our sample periods spend less than 30% of their annual life cycles on their breeding grounds. All of these species are Nearctic-Neotropic migrants (Table 2).

Route selection.—If migrants proceeded directly north in spring, reproduced on their breeding grounds, and returned directly south, captures at a single stopover site would show (on average) more birds (higher capture rates) in autumn than in spring due to the production of young. Although we know that seasonal movements are not so simplistic (e.g., see Rappole et al. 1979), in general migrants at our site showed this predicted relationship (Tables 2 and 3). Several species departed from this trend, however, suggesting that they use different migratory routes. Those species adequately encompassed by our study period that showed greater capture rates in spring than autumn were the Least Flycatcher, Gray-cheeked Thrush, Blue-winged Warbler, Yellow Warbler, Northern Waterthrush, Common Yellowthroat, and Indigo Bunting (Table 2). Relationships of this nature are expected if routes shift seasonally and the banding site lies in a zone near an edge of the autumn route, but well within the spring route.

Several species were not captured at our site in spring, but were captured in autumn: Yellow-throated Vireo, Northern Parula, Cape May Warbler, Black-throated Blue Warbler, and Bay-breasted Warbler (Table 2). This relationship is expected when the site lies outside (or nearly outside) the spring route, but somewhere within the autumn route. Although we say "the" autumn or spring route, we are aware that migration can differ in timing and route selection for sex, age, and population groups (see Phillips 1951, Ramos 1988). We are concerned here, however, with broad, species-level questions, which remain poorly understood (see, for example, Hussell 1980 vs Rappole et al. 1979 and Murray 1989 vs other authors for conflicting hypotheses concerning autumn routes of the Least Flycatcher and Blackpoll Warbler, respectively).

If our sampled habitats were not adequately diverse, a seasonal habitat preference shift could cause fewer captures in autumn, affecting our con-

TABLE 3

DISTRIBUTIONS OF MEAN CAPTURE RATES AMONG HABITATS ON DAYS OF SIMULTANEOUS SAMPLING (RECAPTURES EXCLUDED, ALL YEARS INCLUDED). THE TOP HALF OF THE TABLE COMPARES THE FOUR MOST THOROUGHLY STUDIED HABITATS, WHILE THE LOWER HALF INCLUDES THE LESS STUDIED FIFTH (OAKS)

		Capture rates (SD)[b]						
Season	N[a]	Swamp	Floodplain	Willow	Upland		F	P
Spring	70	126.1 (107.7)	84.4 (71.0)	56.2 (60.3)	25.6 (36.5)		23.69	<0.00005
Autumn	57	347.7 (303.8)	203.8 (225.4)	91.7 (95.7)	50.0 (60.8)		25.92	<0.00005
		Swamp	Floodplain	Willow	Oaks	Upland		
Spring	33	134.5 (129.0)	91.9 (89.4)	71.5 (73.8)	66.9 (89.0)	27.3 (44.0)	6.32	0.0001
Autumn	23	403.5 (418.5)	245.9 (327.8)	108.3 (131.7)	167.0 (191.6)	65.1 (85.8)	5.95	0.0002

[a] Number of days on which habitats considered were sampled simultaneously.

[b] Birds per 1000 net-h, recaptures excluded.

[c] Members of underscored groups are not significantly different from one another; different underscorings represent groups significantly different from one another at the 0.05 level (ANOVA).

clusions regarding species showing apparent seasonal route differences. Our selection of habitats, however, encompassed the wooded types available, and we feel that this factor did not cause the majority of the observed abundance anomalies. The idea that a "narrow" array of sampled habitats caused seasonal differences in capture rates has the most plausibility for the Common Yellowthroat (a species not strictly associated with woodlands), but Floodplain and Swamp had dense breeding populations of this species, so habitat suitable for breeding (at least) was sampled.

The Least Flycatcher, Common Yellowthroat, and Indigo Bunting were inconsistent from year to year in relative seasonal abundance, perhaps a weather-related phenomenon (unpubl.). Blue-winged and Yellow warblers were relatively uncommon at our site (Table 2). In addition, the latter is an early autumn migrant (Janssen 1987). Ely (1970) found the Least Flycatcher to be more common in spring than autumn in west-central Kansas, and the expected "greater in autumn" capture rates occur in western Pennsylvania (Clench and Leberman 1978). These relationships are consistent with the route for this species proposed by Rappole et al. (1979:210, Route 5), wherein the spring route lies generally west of the autumn (primarily trans-Gulf) route. Northern populations of the Indigo Bunting may follow a narrower autumn route that falls within a wider spring route, as suggested by more encounters in spring than autumn both at our site and at Powdermill in western Pennsylvania (Clench and Leberman 1978; see also Ralph 1981). Further south, this species may follow a route similar to that of the Least Flycatcher, but with a more pronounced eastward trend over the Gulf of México and southern Florida (see data in Rappole and Warner 1976, Crawford 1981).

The Northern Waterthrush and Gray-cheeked Thrush showed consistent seasonal abundance imbalances (unpubl.), and the two species may follow similar routes. Rappole et al. (1979:203) considered that both species followed an easterly, primarily trans-Gulf autumn route, although we note that both species occur in both seasons in southern Florida (Crawford 1981). Our data suggest that the eastwardly autumn trend in both species begins far north of the Gulf of México, although western populations of the Northern Waterthrush probably follow a different route (cf Grinnell 1915, Phillips et al. 1964, Oberholser 1974:773).

Two of the five species noted above that were not captured in spring but which appeared in autumn showed a high percentage of young birds in the overall sample, a factor which Ralph (1981) considered an edge-of-route phenomenon (often encountered in coastal areas). In the Cape May and Black-throated Blue warblers, immatures made up 89% and 91%, respectively, of the autumn captures (N = 47 and 11; Table 2), suggesting that our site might fall along the western edge of these species' autumn routes in our region. Janssen (1987) suggested that the Black-throated Blue Warbler arrives and departs the state from the east; our data imply that this species and the Cape May might follow similar regional routes, with a large east-west component, but with either a widening of the autumn route or a stronger southward autumn component. The same general conclusion might also apply to the Northern Parula and Bay-breasted Warbler. However, the lower average immature composition (Northern Parula: 69.2%, N = 13; Bay-breasted Warbler: 75.5%, N = 184), suggests that our site lies further within the autumn routes of these species than those of the previous two. This conclusion is particularly relevant to the Bay-breasted Warbler, given its autumn abundance at our site. Unlike the previous four species, the Yellow-throated Vireo breeds in areas near our site (Janssen 1987), and in spring our nets failed to capture individuals known to be present as transients (pers. obs.). Thus, without further data we cannot determine whether this species shows seasonal route shifts in relation to our site or whether it is typical of the majority of species: simply more common in autumn than in spring.

Habitat selection.—Standard mist nets can only sample a vertical stratum of about 2.5 m. Interpretations of capture rates between habitats with different canopy heights must therefore consider that different percentages of the vegetative stratum have been sampled in each habitat. For ground-foraging species this is not a problem, but most of the species captured at our site forage (at aboveground or near-ground levels). Our average capture rates in each habitat do show a strong relationship with mean canopy height (Table 3, Appendix), so we cannot determine which habitat(s) are preferred overall. It is clear, however, that seasonal changes in distribution do occur at our site (Table 3). These differences are due to disproportionate increases in capture rates between spring and autumn in each habitat. In general, a greater percentage of the overall autumn increase at our site occurred in the Swamp and Floodplain than in the other three habitats. If we consider the four habitats netted most thoroughly (and in parentheses the lesser number of days upon which all five habitats were sampled simultaneously; both from Table 3), average spring capture rates represented a varying percentage of average autumn capture rates for each habitat: Swamp 36.2% (33.3%), Floodplain 41.4% (37.4%), Willows 61.3% (66.0%), Upland 51.2% (41.9%), and Oaks (40.0%).

Are measured habitat variables correlated with the observed seasonal shifts in distribution? The high variability of daily capture rates (see standard deviations, Table 3) makes it difficult to assess possible correlations between seasonal increases in capture rates (above) and habitat-related parameters (Appendix). Individuals of the more common migrant species at our site were captured in most, if not all, of the habitats sampled (unpubl.). Of the woody vegetation, only two shrub taxa were shared as a common feature among the five sampled habitats: dogwoods (*Cornus* spp.) and buckthorn (*Rhamnus catharticus*), an exotic species common at our site (Appendix). The seasonal increases in capture rates showed no relationship to dogwood densities, but may be related to buckthorn densities. The habitat showing the least increase in autumn captures (Willows) has the highest density of buckthorn, and that with the greatest autumn increase (Swamp) has the lowest density of this species (visual examination of mean capture rates vs mean buckthorn densities). The meaning of this relationship requires a more detailed analysis (net-by-net) than we can present here.

Swamp and Floodplain were the wettest of the five habitats (not quantified), and also had the greatest ground cover and least canopy cover (Appendix). These habitats showed the highest increases in capture rates between spring and autumn. The disproportionate seasonal capture rate increases do not appear to be related to canopy height or any of the other four measured structural characteristics. Thus, if foraging height does not change seasonally in a habitat-specific manner (something we cannot address), our data suggest that the avian community as a whole undergoes a seasonal shift in habitat use at this site.

DISCUSSION

It is impossible to estimate what percentage of birds occurring in a habitat are captured, but it is clear (Fig. 1) that our small forested patches were used by a considerable number of migrants during our study. This occurrence, together with our finding that a seasonal spatial shift in distribution occurs among these habitats, suggests that a diverse array of forest fragments may serve an important role to stopover migrants. No habitat at our site could be singled out as being "best" for woodland-associated migrants. The coincidence of median dates among many species (Table 2), the numbers of birds present, and the relatively short period of time in which migration occurs (Table 2, Fig. 1) suggest that seasonal demand on the resources at this site is acute. Several decades of invertebrate abundance data for deciduous woods approximately 680 km SE of our site show two pronounced annual peaks, occurring in May and September (Kendeigh 1979:35), suggesting that Nearctic deciduous woodlands may have higher levels of invertebrate food resources available during migrant passage than at other times of the year. Further data (and better geographic concordance) would be required to determine whether the timing of migration in the species considered here is affected by the availability of food at potential stopover sites.

Demonstrations of seasonal shifts in habitat use by migrant passerines are rare (Jones 1895; Hutto 1985; Winker et al. 1992), but this may be because they have not been looked for. We are not aware of another study that has demonstrated a seasonal spatial shift in the avian community as a whole at a stopover site. The seasonal shifts in the distribution of capture rates among our sampled habitats (Table 3) are of a somewhat uncertain nature, because habitats of different canopy heights are not equivalently sampled by mist nets. While these analyses show that some spatial shifts occurred, we cannot determine whether these changes were caused by two-dimensional shifts (seasonal changes in habitat use) or three-dimensional shifts (seasonally different foraging levels causing different capture susceptibilities among habitats with variable canopy heights). The lack of correlation between relative seasonal increases in capture rates and canopy height suggests that two-dimensional shifts are a more important factor. We know that for at least two ground or near-ground level foragers (Swainson's Thrush and the Northern Waterthrush), two-dimensional shifts are occurring (Winker et al. 1992), although neither of the patterns of seasonal change shown by these common species matches that of the overall avian community. The seasonal changes in distribution shown at our site could be caused by seasonal changes in habitat use alone or in combination with seasonal shifts in foraging heights.

The eastward trends in autumn migration noted for the Northern Waterthrush and Gray-cheeked Thrush raise questions. *Why* such an eastward swing should occur well north of the nearest ecological barrier (Gulf of México) in only two of the species encountered commonly at our site will likely remain a mystery until we can discover more about the movements of these species and others with similar (and dissimilar) breeding and wintering ranges.

When placed across a variety of available habitats, mist nets allow a quantification of migrant abundance, timing, and habitat preference(s) at a stopover site. Summary statistics from these sites are few, but, as shown here, can be useful in illuminating local and regional patterns of passerine migration. Only when such summaries are available across a broader geographic area can we hope to understand specific migration strategies at the regional and continental levels.

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Appendix I

Vegetative Structure and Composition of Each Sampled Habitat

Primer.—Species of trees: Figures after each give number of trees/ha, relative density (%), relative dominance (%), and frequency of sample circles at which species occurred (%), in that sequence. Size class information: Tree diameter size classes are as follows (conversion directly from inches-based methodology allows direct comparison to an established literature base): *A* (7.6–15.2 cm), *B* (15.2–22.9 cm), *C* (22.9–38.1 cm), *D* (38.1–53.3 cm), *E* (53.3–68.6 cm), and *F* (68.6–83.8 cm). Figures after each size class give number of trees/ha of that class, relative density (%), basal area (m^2/ha), and relative dominance (%). Shrubs by taxon: Figures after each give relative density (%) and frequency of circles at which taxon occurred (%).

1. *Floodplain.*—Trees 7.6 cm diameter and over, 443/ha; total basal area, 16.5 m^2/ha. Species comprising 90% of the total number of trees: *Salix nigra,* 186.9, 42.2, 66.9, 100; *Ulmus americana,* 99.5, 22.5, 10.5, 92; *Acer saccharinum,* 92.4, 20.9, 11.6, 62.5; *Acer negundo,* 22.1, 5.0, 1.5, 25. Trees by diameter size class: *A* 160.8, 36.3, 1.5, 9; *B* 165.8, 37.4, 4.6, 28; *C* 100.5, 23.7, 7.5, 45; *D* 14.1, 3.2, 2.4, 14.3; *E* 2.0, 0.5, 0.6, 3.5. Shrub stems/ha, 18,430 (est.). Shrub taxa comprising 90% of the total number of shrubs: *Rhamnus catharticus,* 38.6, 95.8; *Cornus* spp., 31.9, 100; *Alnus rugosa,* 10.0, 41.7; *Salix* sp., 5.7, 45.8; *Acer negundo,* 3.1, 75. Ground cover, 88%; canopy cover, 50%; mean canopy height, 13.1 m (range 4.6–18.3 m).

2. *Swamp.*—Trees 7.6 cm diameter and over, 53/ha; total basal area, 1.2 m^2/ha. Species comprising 90% of the total number of trees: *Ulmus americana,* 18.1, 34.6, 21, 33.3; *Betula papyrifera,* 16.1, 30.8, 29, 16.6; *Salix nigra,* 10.1, 19.2, 40.3, 25; *Populus tremuloides,* 4, 7.7, 6.5, 8.3; *Acer saccharinum,* 2, 3.9, 1.6, 8.3. Trees by diameter size class: *A* 26.1, 41.7, 0.2, 21; *B* 22.1, 35.3, 0.6, 53.2; *C* 4, 6.4, 0.3, 25.8. Shrub stems/ha, 20,052 (est.). Shrub taxa comprising 90% of the total number of shrubs: *Alnus rugosa,* 36.4, 91.7; *Cornus* spp., 21.2, 100; *Betula pumila,* 13.3, 50; *Salix* sp., 12.8, 100; *Rhamnus catharticus,* 8, 58.3. Ground cover, 90.8%; canopy cover, 20%; mean canopy height, 4.8 m (range 1.5–9.1 m).

3. *Upland.*—Trees 7.6 cm diameter and over, 729/ha; total basal area, 24.6 m^2/ha. Species comprising 90% of the total number of trees: *Populus tremuloides,* 198.2, 27.2, 18.8, 44.4; *Quercus alba,* 158.2, 21.7, 35.3, 72.2; *Betula papyrifera,* 124.6, 17.1, 12.8, 72.2; *Tilia americana,* 65.6, 9, 5.8, 83.3; *Quercus rubra,* 53.5, 7.4, 15.4, 66.7; *Prunus serotina,* 33.5, 4.6, 4.2, 66.7; *Ostrya virginiana,* 26.8, 3.7, 1.1, 27.8. Trees by diameter size class: *A* 304, 41.7, 2.8, 11.5; *B* 262.6, 36, 7.3, 29.8; *C* 136.7, 18.8, 10.1, 41.4; *D* 25.6, 3.5, 4.3, 17.3. Shrub stems/ha, 4561 (est.). Shrub taxa comprising 90% of the total number of shrubs: *Rhamnus catharticus,* 34.9, 100; *Tilia americana,* 16.6, 83.3; *Prunus* spp., 11.5, 61.1; *Cornus* spp., 9.5, 55.6; *Acer negundo,* 8.8, 88.9; *Ostria virginiana,* 5.9, 38.9; *Populus* spp., 2.79, 27.8. Ground cover, 61.4%; canopy cover, 83.1%; mean canopy height, 16.8 m (range 13.7–21.3 m).

4. *Willows.*—Trees 7.6 cm diameter and over, 553/ha; total basal area, 24.3 m^2/ha. Species comprising 90% of the total number of trees: *Populus tremuloides,* 154.7, 28, 14.9, 75; *Salix nigra,* 102.5, 18.6, 56.4, 41.7; *Acer saccharinum,* 92.4, 16.7, 9.3, 58.3; *Prunus virginiana,* 58.3, 10.6, 4.9, 33.3; *Ulmus americana,* 40.2, 7.3, 2.5, 50; *Acer negundo,* 30.1, 5.5, 2.2, 50; *Quercus rubra,* 22.1, 4, 3.2, 50. Trees by diameter size class: *A* 248.3, 85.8, 1.9, 7.9; *B* 255.6, 88.3, 5.9, 24.5; *C* 91.6, 31.7, 5.7, 23.4; *D* 57.9, 20, 8.1, 33.3, *E* 7.2, 2.5, 1.7, 7.2; *F* 2.4, 0.8, 0.9, 3.8. Shrub stems/ha, 21,388 (est.). Shrub taxa comprising 90% of the total number of shrubs: *Rhamnus catharticus,* 58.2, 100; *Cornus* sp., 12.6, 83.3; *Ribes* spp., 9.53, 75; *Corylus* sp., 4.7, 58.3; *Ulmus americana,* 3.3, 100; *Acer negundo,* 3.1, 75. Ground cover, 70.4%; canopy cover, 68.3%; mean canopy height, 15.2 m (range 12.2–21.3 m).

5. *Oaks.*—Trees 7.6 cm diameter and over, 581/ha; total basal area, 24.6 m^2/ha. Species comprising 90% of the total number of trees: *Quercus macrocarpa,* 306.2, 52.7, 42.7, 100; *Quercus rubra,* 178.4, 30.1, 48.2, 90; *Prunus serotina,* 36.2, 6.2, 1.9, 50; *Populus tremuloides,* 21.7, 3.7, 3.5, 20. Trees by diameter size class: *A* 159.1, 27.4, 1.5, 5.5; *B* 221.8, 38.2, 6.2, 22.9; *C* 159.1, 27.4, 11.8, 43.7; *D* 38.6, 6.6, 6.5, 23.9; *E* none; *F* 2.4, 0.4, 1.1, 4.1. Shrub taxa comprising 90% of the total number of shrubs: *Rhamnus catharticus,* 52.1, 100; *Cornus* spp., 15.5, 100; *Corylus* sp., 10.6, 90; *Ribes* spp., 9.42, 80; *Prunus* spp., 3.3, 90. Ground cover, 62%; canopy cover, 82%; mean canopy height, 14.5 m (range 11.3–15.2 m).