

HABITAT USE AND BEHAVIOR OF MIXED SPECIES LANDBIRD FLOCKS DURING FALL MIGRATION

PAUL G. RODEWALD^{1,2,3} AND MARGARET C. BRITTINGHAM¹

ABSTRACT.—Little research has examined the ecology of mixed species flocks of migrant and resident landbirds during migratory periods. We studied habitat use and behavior of mixed species insectivorous landbird flocks during fall migration in central Pennsylvania. From late August to early October, 1998 and 1999, 220 flocks were observed for 30-min periods in six forest habitat types: mature forest interior, mature forest edge, mature forest agricultural edge, mature suburban forest, pole stage forest, and shrub/sapling stage forest. Sixty species were recorded in flocks that contained 2–24 species each (mean = 9.25 ± 0.29 SE). Flocks contained 2–181 individuals (mean = 22.12 ± 1.18 SE). Flocks in the six habitats had 49–61% Nearctic-Neotropical migrant individuals, 5–15% temperate migrants, and 23–37% residents. Abundance and species richness of migratory guilds (Nearctic-Neotropical migrants, temperate migrants, and resident species) within flocks were highest in structurally heterogeneous habitats (especially forest edge habitat) and were lowest in homogeneous pole stage forest. Of nine migrant species whose abundance varied significantly among habitats, six had highest abundance in flocks in forest edge habitat: Blue-headed Vireo (*Vireo solitarius*), Red-eyed Vireo (*V. olivaceus*), Blue-gray Gnatcatcher (*Poliophtila caerulea*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Black-throated Green Warbler (*D. virens*), and Magnolia Warbler (*D. magnolia*). Resident parids (Black-capped Chickadee, *Poecile atricapillus*, and/or Tufted Titmouse, *Baeolophus bicolor*) occurred within 82% of flocks and were observed leading 68% of these flocks. Movement rate (m/min) of flocks varied among habitats with flocks in edge-dominated habitats (forest edge, forest agricultural edge, and suburban forest) tending to have slower movement rates than in pole stage forest and forest interior, suggesting that food availability may have been greater in edge-dominated habitats. Consistently high species richness and abundance of migrant guilds and individual species strongly suggests that structurally diverse forest edge habitats were selected and provided relatively high quality stopover habitat for landbirds during fall migration. Received 19 December 2000, accepted 20 October 2001.

Birds face numerous challenges while migrating between breeding and nonbreeding locations. Aside from high energetic costs during migration, migrants must adjust to poor weather and unfamiliar habitats, compete with other migrant and resident birds, and avoid predators (Moore et al. 1995). Selection of high quality habitat during migration should allow migrants to face such challenges and meet energy requirements more efficiently, thereby increasing their chances for a successful migration. For example, in the Rio Grande Valley of New Mexico, Wilson's Warblers (*Wilsonia pusilla*) occurring in high quality stopover habitat (native willows) had higher rates of fat deposition and shorter stopover periods than in low quality habitat (Yong et al. 1998). Despite the importance of stop-

over habitat for migrants, there is surprisingly little information on patterns of habitat use and habitat quality during migration in North America (see Petit 2000 for a review).

Because both Nearctic-Neotropical and temperate migrant landbirds regularly join resident species in mixed species flocks during migration (Morse 1989), assessing differences among habitats in migrant abundance, species richness, and behavior within these flocks should provide information on important stopover habitats for migrants. However, very few studies have examined ecology or species composition of flocks in migration (but see Keast 1980, Morse 1989). Previous studies during migration (irrespective of flocks) have demonstrated that migrants select among available habitats and their abundance often is positively correlated with resource availability (reviewed in Moore et al. 1995 and Petit 2000), including both insects (Hutto 1985, Blake and Hoppes 1986) and fruit (Martin 1985, Blake and Hoppes 1986, Suthers et al. 2000). Given the importance of food resources to migrating birds, these studies suggest that habitats in which migrants are most abundant

¹ School of Forest Resources and Intercollege Graduate Program in Ecology, The Pennsylvania State Univ., University Park, PA 16802, USA.

² Current address: School of Natural Resources, The Ohio State Univ., Columbus, OH 43210, USA.

³ Corresponding author; E-mail: rodewald.2@osu.edu

typically should be high quality stopover habitats. Migrant species richness also may be an indicator of migrant habitat quality. For example, on Horn Island off the coast of Mississippi, species richness and abundance of spring migrants were highest in scrub/shrub habitat (Moore et al. 1990), which is thought to be the most suitable habitat for replenishing fat stores (Moore and Aborn 2000).

We propose that flock behavior (i.e., movement rate) could provide an indirect measure of relative food availability within habitats and complement data on abundance and species richness. Flock movement rates often are recorded in studies of mixed species flocks, but typically have not been related to habitats or habitat quality. Morse (1970) noted that mixed species flocks moved more rapidly through unfavorable habitats, though he provided no data on the subject. However, there are reasons to expect such a relationship. Foraging speed (number of movements/min) of individual birds increases where food availability is low because birds that forage faster search larger amounts of substrate and increase their prey encounter rate (Robinson and Holmes 1982). For example, Lovette and Holmes (1995) found that American Redstarts (*Setophaga ruticilla*) foraged faster in Jamaican wintering habitats, where food availability was relatively low, than in Nearctic breeding habitats. In addition, Hutto (1990) suggested that movement rate (distance moved/time) of individuals should be negatively related to food availability, perhaps due to area restricted searching following successful prey attacks. Because prey handling time should increase in habitats with high food availability, we further expect this to lower an individual's movement rate. Although movement rates of individuals may not be directly related to those of mixed species flocks, such a relationship seems likely and, thus, we propose that flocks will move more slowly in habitats of high food availability.

We used abundance, species richness, and behavior of mixed species foraging flocks as indicators of habitat quality within six forest habitat types in central Pennsylvania. These habitats varied in local habitat structure and landscape characteristics (forest, suburban, or agricultural landscape matrix) and represent habitats that are commonly encountered by

migrating landbirds in eastern North America. Specifically, we compared abundance of migratory guilds and individual species, species richness and composition, and movement rates of mixed species flocks among habitats to identify important habitats for migrating landbirds in inland areas. We expected that relatively high quality habitat would be indicated by a combination of high abundance and species richness of migrants within flocks and lower flock movement rate.

STUDY AREA AND METHODS

Study area.—We studied mixed species landbird flocks from 21 August to 10 October, 1998–1999, within the Ridge and Valley Province of Centre and Huntingdon counties, Pennsylvania (40° 42' N, 77° 55' W). Study areas included Rothrock State Forest, State Game Lands 176, suburban forests in the State College area, and private land. We sampled mixed species flocks within six mixed hardwood forest habitat types (forest interior, forest edge, forest agricultural edge, suburban forest, pole stage forest, and shrub/sapling stage forest; described below) that varied in local habitat structure and/or landscape characteristics (forest, suburban, or agricultural landscape matrix). Additional description of the study area is given in Rodewald (2001).

Habitat types.—Four mature forest habitats (forest interior, forest edge, forest agricultural edge, and suburban forest) varied in their landscape characteristics, and typically were 80–100 years old, 20–30 m tall, with largely unbroken canopies. Small canopy gaps resulting from one to several tree falls or unimproved roads (10–15 m wide) were not considered edge habitats because the forest canopy remained largely intact. Mature forests were the most vertically heterogeneous habitats (i.e., with canopy, midstory, and understory layers). However, forest interior habitat often was less vertically heterogeneous than other mature forests because understory shrubs and saplings usually were sparser. Forest interior habitat was located within forest-dominated landscapes.

Forest edge habitat also was located within forest-dominated landscapes and occurred at edges between mature forest and large forest openings with regenerating shrubs and saplings, e.g., power line right-of-ways, open canopy roads (>20 m wide), and regenerating clearcuts. Forest edge habitat had dense understory foliage along the edge, and a gradual edge (typically 5–15 m wide) between mature forest and shrub/sapling stage habitat.

Forest agricultural edges were located within a forest-agricultural landscape matrix and characterized by an abrupt edge (≤5 m wide) between an agricultural crop and mature forest. Forest agricultural edges had distinctly lower amounts of understory vegetation associated with the edge than the forest edge habitat type.

Suburban forest habitats were 6- to 14-ha mature forest stands dispersed within lightly wooded suburban housing developments and had relatively large amounts of edge habitat due to their small size. Therefore, we considered suburban forests to be edge-dominated habitats, similar to forest edge and forest agricultural edge habitats.

Pole stage forest habitats were within forest-dominated landscapes and were even-aged stands approximately 30 years old, <15 m tall, and with trees 10–25 cm diameter (dbh). These forests had a dense canopy with little understory vegetation and thus were not vertically heterogeneous in habitat structure.

Shrub/sapling stage forest habitats (i.e., early successional forests) were regenerating forest cuts within forest-dominated landscapes. These habitats had shrubs and saplings mostly 2–4 m tall and <8 cm dbh, and occasional larger trees \leq 15 m tall. Shrub/sapling stage habitats lacked the vegetation layering of mature forest habitats, but did have a highly variable canopy layer due to differing heights of shrubs, saplings, and trees.

Plant species composition of habitats.—Common to fairly common tree species of study habitats included white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), black birch (*Betula lenta*), and hickories (*Carya* spp.). Conifers such as eastern white pine (*Pinus strobus*), pitch pine (*P. rigida*), and eastern hemlock (*Tsuga canadensis*) were less common in the study area. Common to fairly common woody understory plants of forest interior, forest edge, and forest agricultural edge included saplings of canopy tree species (especially red maple), as well as blueberries (*Vaccinium* spp.), mountain laurel (*Kalmia latifolia*), and witch-hazel (*Hamamelis virginiana*). Non-native bush honeysuckles (*Lonicera* spp.), common privet (*Ligustrum vulgare*), and red maple saplings were most common in suburban forest understory.

Flock observations.—During fall, the patchy distribution of mixed species bird flocks and the lower detectability of less vocal migrants made traditional bird survey methods (e.g., point-counts, line-transects) less efficient for documenting migrant habitat use patterns. Thus, we recorded habitat use and behavioral data while following mixed species bird flocks. We defined mixed species flocks as an assemblage of two or more species occurring <25 m of each other and moving together during an observation period (Hutto 1987). We examined insectivore flocks that contained \geq 1 migrant species and often moved widely during an observation period. We did not collect data on mixed species flocks of *Catharus* and *Hylocichla* thrushes and other species that are strongly frugivorous during fall (Parrish 1997, 2000); such flocks were more sedentary and focused their foraging effort within areas with fruiting plants. However, several species, including Red-eyed Vireo (*Vireo olivaceus*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*), occurred in

both frugivore and insectivore flocks. Similarly, we did not examine mixed species flocks of granivorous species (e.g., sparrows).

We observed flocks from 06:00–16:00 EST, but 85% of flock observations were made prior to 12:00. We sampled flocks equally across habitats with respect to time of day. Flocks were located by walking through study habitats while listening for call notes of flock members and searching visually for birds. We followed flocks for up to 30 min when possible. After sampling a flock, we were careful not to resample the same flock and typically moved >250 m from the location before collecting additional data. Sampling of flocks was done over extensive areas and not at specific sites that were regularly revisited. On occasions when the same general area was resampled, several days had elapsed since the previous visit. Given this pattern of sampling, it seems very unlikely that we observed the same flock of individuals more than once on the same or different days.

We recorded species richness and abundance of species that attended mixed species flocks. When it was not possible to count each flock member during an observation period, we made a conservative estimate of the number of additional birds in the flock. At 2-min intervals, we visually estimated the distance from the center of the flock to the nearest habitat edge, and recorded flock activity (e.g., foraging, resting) and habitat type used. At the end of an observation, we estimated total distance traveled by the flock by pacing the path taken by the flock back to the starting point of the observation.

Nearly all flocks used a single habitat type during an observation period. On occasions when flocks used more than one habitat, they were categorized as using the habitat in which they spent the majority of the observation period. We considered flocks to be using forest interior habitat when their mean distance to a habitat edge was >50 m and the flock did not use edges during an observation period. We considered flocks to be using edge habitats (i.e., forest agricultural edge and forest edge) if their mean distance to the habitat edge was <50 m during an observation period.

We recorded whether parids (Black-capped Chickadee, *Poecile atricapillus*, and/or Tufted Titmouse, *Baeolophus bicolor*) led flocks. Parids were considered to lead flocks when an individual(s) flew from an area of flock foraging activity to a new area, and was promptly followed by flights of other flock species oriented in the same direction (Morse 1970). Because only unambiguous observations of leading were collected, our estimates of leading by parids represent minimum values (Morse 1970).

Statistical analysis.—We classified flocking species as Nearctic-Neotropical migrants following DeGraaf and Rappole (1995), with the exception that Blue-headed Vireo (*Vireo solitarius*), Golden-crowned Kinglet (*Regulus satrapa*), Ruby-crowned Kinglet (*R. calendula*), Yellow-rumped Warbler (*Dendroica coronata*), and Pine Warbler (*D. pinus*) were classified as temperate migrants because they winter mainly

north of 25° N (American Ornithologists' Union 1998, Poole and Gill 1993–2001); remaining species were classified as temperate migrants or residents (American Ornithologists' Union 1998; Table 1). For each flock observed, we calculated species richness for all species combined (i.e., total richness) and for each migratory guild. We calculated abundance for all species combined (i.e., total abundance), migratory guilds, and individual species. Using only flock observations lasting >15 min, we calculated mean movement rate and mean distance to nearest habitat edge for each flock.

We conducted statistical analyses using SAS software (SAS Institute, Inc. 1990). We checked data for normality and homogeneous variance, and variables that did not meet assumptions for parametric tests were log transformed. Statistically significant results were indicated at $P < 0.05$. In the absence of significant annual differences, we pooled flock data across years. For each migratory guild and for all species combined we examined differences in species richness and abundance among habitats using analysis of covariance (ANCOVA) with habitat type as the main factor and time of day as a covariate. We used this same analysis to test for differences among habitats in the abundance of individual species within flocks (only species with ≥ 15 observations were included). ANCOVA also was used to examine differences in flock movement rate among habitats, with covariates being total abundance within flock and time of day. Total abundance was included to control for the effect of flock size because this is positively related to flock movement rate (Morse 1973). Time of day was included as a covariate because there was a negative correlation between time of day and most measures of species richness, abundance, and flock movement rate. When we obtained a significant result in the above analyses, we made pairwise comparisons among habitats using ANOVA, and controlled experimentwise error at 0.05 using the Bonferroni method. We used correlation analysis to test for a relationship between distance to nearest habitat edge and time of day for flocks that occurred in the three edge-dominated habitats (forest edge, forest agricultural edge, and suburban forest).

RESULTS

We observed 220 flocks in the six habitat types during fall 1998 and 1999. Sample sizes for flocks in each habitat were forest interior (57), forest edge (41), forest agricultural edge (38), suburban forest (30), pole stage forest (21), and shrub/sapling stage forest (33). Flocks included nonbreeding transient species (e.g., Bay-breasted Warbler, *Dendroica castanea*), both transient and postbreeding individuals of migratory species that bred locally (e.g., Black-throated Green Warbler, *D. virens*), and resident species. Individuals within flocks occasionally were observed preening or resting, but spent the large majority of their

time actively foraging. Flock members foraged primarily on arthropods during observation periods. Some individuals did consume fruit; however, flocks did not linger in fruiting trees or shrubs. Of migratory species we studied, few lone individuals were encountered outside flocks, suggesting a strong propensity to flock during fall stopover for these migrant landbirds.

We observed 167 flocks for ≥ 15 min. Within the three edge-dominated habitats (forest edge, forest agricultural edge, and suburban forest), there was a positive relationship ($r = 0.25$, $P = 0.017$, $n = 86$) between distance to nearest edge habitat and time of day, such that flocks foraged closer to edges during morning. In addition, flocks in edge-dominated habitats typically spent the entire observation period <10 m from the actual habitat edge.

Species richness within flocks.—We recorded 60 species attending mixed species insectivorous bird flocks, including 41 Nearctic-Neotropical migrant species, 13 temperate migrant species, and six resident species. Individual flocks contained 2–24 species with a mean of 9.25 (± 0.29 SE) species. No significant interaction between habitat and year was detected for species richness of Nearctic-Neotropical migrants ($P = 0.74$), temperate migrants ($P = 0.56$), or resident species ($P = 0.59$), so richness data were pooled by year for each guild. Both total richness ($F_{5,213} = 11.51$, $P < 0.001$) and richness of Nearctic-Neotropical migrants ($F_{5,213} = 4.28$, $P = 0.001$) within flocks differed among habitats and were highest in forest edge and lowest in pole stage forest (Table 2); time of day was a significant covariate for both total richness ($P = 0.008$) and richness of Nearctic-Neotropical migrants ($P = 0.013$). Species richness of temperate migrants varied ($F_{5,213} = 4.04$, $P = 0.002$) among habitats and was highest in flocks in both forest interior and forest edge and lowest in pole stage forest (Table 2), but did not vary significantly with time of day ($P = 0.87$). Resident species richness differed ($F_{5,213} = 11.24$, $P < 0.001$) among habitats and was highest in forest edge and lowest in flocks in pole stage forest (Table 2), but did not vary significantly with time of day ($P = 0.17$).

Guild and total abundance within flocks.—Single flocks contained 2–181 individuals

with a mean of 22.12 (± 1.18 SE) individuals. Individual flocks had 49–61% Nearctic-Neotropical migrants, 5–15% temperate migrants, and 23–37% residents. No significant interactions between habitat and year were detected for abundance of Nearctic-Neotropical migrants ($P = 0.83$), temperate migrants ($P = 0.20$), and residents ($P = 0.59$), so abundance data were pooled by year for each guild. Abundance of both Nearctic-Neotropical migrants ($F_{5,213} = 6.30$, $P < 0.001$) and all species combined (i.e., total abundance; $F_{5,213} = 12.66$, $P < 0.001$) differed among habitats and were highest in flocks in forest edge, whereas flocks in pole stage forest had only one quarter as many individuals; abundance of Nearctic-Neotropical migrants and all species combined were intermediate within flocks in remaining habitats (Table 2). Time of day was a significant ($F_{1,213} = 6.61$, $P = 0.011$) covariate and was negatively related to Nearctic-Neotropical migrant abundance. Abundance of temperate migrants within flocks differed ($F_{5,213} = 4.80$, $P < 0.001$) among habitats with highest numbers in forest interior and lowest numbers in pole stage forest (Table 2). Resident abundance within flocks differed ($F_{5,213} = 5.03$, $P < 0.001$) among habitats and was highest in forest edge and lowest in pole stage forests (Table 2).

Abundance of individual species within flocks.—Of 60 species that occurred within flocks, 33 had adequate sample sizes for statistical analysis, and abundance of 12 of these species varied significantly among habitats (Table 1). Of nine migrant species whose abundance varied among habitats, six had highest abundance in flocks in forest edge habitat (Blue-headed Vireo; Red-eyed Vireo; Blue-gray Gnatcatcher, *Poliophtila caerulea*; Chestnut-sided Warbler, *Dendroica pensylvanica*; Black-throated Green Warbler; and Magnolia Warbler, *D. magnolia*), but not significantly different from that in 1–3 other habitats. Downy Woodpeckers (*Picoides pubescens*), White-breasted Nuthatches (*Sitta carolinensis*), and Tufted Titmice were most abundant in the four mature forest habitats. For the habitat types studied, 67% of the 33 species were recorded within flocks in all six habitats, 27% occurred in five habitats, and 6% occurred in only four habitats (Table 1). However, species were heavily skewed in their

abundance and many of the 33 species occurred primarily within 3–4 habitats and were found only a few times (or not at all) in pole stage forest.

Many species that joined flocks were recorded in numbers too low to permit statistical analysis (see Appendix). Of species recorded infrequently within flocks, forest edge habitats had the most species with high mean abundance relative to other habitats, but many species also were abundant in flocks in shrub/sapling stage forest, forest interior, and forest agricultural edges.

Parids occurred in 82% of mixed species flocks and were observed leading at least 68% of these flocks. Abundance of parids within flocks did not differ significantly among habitats or in relation to time of day ($F_{5,213} = 1.68$, $P = 0.14$).

Flock movement rate.—Movement rate of flocks varied among habitats ($F_{5,159} = 2.77$, $P = 0.019$), but there were no significant pairwise differences after Bonferroni adjustment. However, flocks tended to move more rapidly in pole stage forest and forest interior habitats (Fig. 1) than in shrub/sapling stage and edge-dominated habitats (forest edge, forest agricultural edge, and suburban forest). Movement rate was positively associated ($F_{1,159} = 13.33$, $P < 0.001$) with total abundance of birds within flocks, but not with time of day ($F_{1,159} = 2.7$, $P = 0.10$).

DISCUSSION

Migrating insectivorous landbirds in mixed species flocks used structurally heterogeneous habitats more than homogeneous pole stage forests. Among heterogeneous habitats, three lines of evidence suggested that forest edges were selected and provided high quality stop-over habitat for migrating landbirds. First, both flock size (i.e., total abundance) and abundances of many individual species were greatest in forest edges (e.g., power line right-of-ways, open canopy forest roads, edges of forest cuts). In addition, bird survey data (Rodewald 2001) collected along transects in these habitats during fall indicated that edge-dominated habitats had significantly more flocks than other habitats.

Second, species richness within flocks typically was higher in forest edges than in other habitat types. In contrast, pole stage forests

TABLE 1. Abundance per flock for individual species that occurred within mixed species landbird flocks in six habitats in the Ridge and Valley Province of central Pennsylvania, fall 1998 and 1999. Flock sample sizes are in parentheses.

Species and migratory guild ^a	Forest interior (57)		Forest edge (41)		Forest agricultural edge (38)		Suburban forest (30)		Pole stage forest (21)		Shrub/sapling stage forest (33)		ANCOVA P
	Mean	SE ^b	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>) ^R	0.03	0.02	0.20	0.11	0.18	0.08	0.20	0.07	0.00	0.00	0.00	0.00	0.087
Downy Woodpecker (<i>Picoides pit-bescens</i>) ^R	0.69	0.10 ^A	0.77	0.12 ^A	0.63	0.10 ^{AB}	0.57	0.13 ^{AB}	0.05	0.05 ^B	0.27	0.10 ^B	<0.001
Hairy Woodpecker (<i>P. villosus</i>) ^R	0.19	0.07	0.22	0.08	0.05	0.04	0.03	0.03	0.05	0.05	0.03	0.03	0.074
Eastern Wood-Pewee (<i>Contopus virens</i>) ^N	0.52	0.13	0.65	0.17	0.55	0.18	0.40	0.14	0.00	0.00	0.36	0.12	0.091
Blue-headed Vireo (<i>Vireo solitarius</i>) ^T	0.50	0.10 ^{AB}	0.72	0.17 ^A	0.13	0.06 ^B	0.33	0.15 ^{AB}	0.14	0.10 ^B	0.45	0.13 ^{AB}	0.009
Philadelphia Vireo (<i>V. philadelphicus</i>) ^N	0.12	0.05	0.15	0.09	0.08	0.04	0.07	0.05	0.05	0.05	0.12	0.07	0.853
Red-eyed Vireo (<i>V. olivaceus</i>) ^N	1.76	0.34 ^{AB}	2.52	0.56 ^A	1.95	0.35 ^{AB}	1.50	0.36 ^{AB}	0.62	0.22 ^B	0.61	0.17 ^B	0.003
Black-capped Chickadee (<i>Poecile atricapillus</i>) ^R	3.09	0.35	3.25	0.43	2.71	0.29	2.03	0.45	2.52	0.49	2.94	0.39	0.469
Tufted Titmouse (<i>Baeolophus bicolor</i>) ^R	0.72	0.17 ^C	1.62	0.24 ^B	1.79	0.26 ^B	2.77	0.37 ^A	0.48	0.26 ^C	0.82	0.27 ^{BC}	<0.001
White-breasted Nuthatch (<i>Sitta carolinensis</i>) ^R	1.05	0.12 ^A	1.05	0.16 ^A	0.89	0.14 ^{AB}	1.07	0.21 ^A	0.00	0.00 ^C	0.36	0.10 ^{BC}	<0.001
Brown Creeper (<i>Certhia americana</i>) ^T	0.26	0.08	0.12	0.10	0.05	0.04	0.17	0.08	0.05	0.05	0.00	0.00	0.155
Golden-crowned Kinglet (<i>Regulus satrapa</i>) ^T	0.67	0.26	0.52	0.22	0.03	0.03	0.20	0.17	0.19	0.15	0.21	0.14	0.255
Ruby-crowned Kinglet (<i>R. calendula</i>) ^T	1.15	0.35 ^A	0.75	0.26 ^{AB}	0.16	0.07 ^B	0.33	0.20 ^{AB}	0.38	0.20 ^{AB}	0.21	0.11 ^{AB}	0.022
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>) ^N	0.14	0.06 ^{AB}	0.35	0.12 ^A	0.05	0.04 ^B	0.10	0.06 ^A	0.00	0.00 ^B	0.06	0.06 ^B	0.012
Tennessee Warbler (<i>Vermivora peregrina</i>) ^N	0.21	0.06	0.22	0.12	0.13	0.07	0.07	0.05	0.09	0.07	0.21	0.10	0.833
Nashville Warbler (<i>V. ruficapilla</i>) ^N	0.17	0.06	0.35	0.13	0.39	0.10	0.13	0.06	0.19	0.09	0.36	0.12	0.311
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>) ^N	0.33	0.10 ^B	1.47	0.37 ^A	0.50	0.14 ^B	0.53	0.17 ^B	0.05	0.05 ^B	1.03	0.21 ^{AB}	<0.001
Magnolia Warbler (<i>D. magnolia</i>) ^N	0.65	0.12 ^B	2.27	0.51 ^A	1.24	0.28 ^{AB}	1.23	0.19 ^{AB}	0.71	0.17 ^B	1.33	0.22 ^{AB}	<0.001
Cape May Warbler (<i>D. tigrina</i>) ^N	0.26	0.10	0.35	0.13	0.39	0.14	0.03	0.03	0.14	0.08	0.61	0.18	0.097
Black-throated Blue Warbler (<i>D. caerulescens</i>) ^N	0.62	0.12	0.27	0.09	0.34	0.11	0.40	0.12	0.43	0.16	0.64	0.17	0.209

TABLE 1. CONTINUED

Species and migratory guild ^a	Forest interior (57)		Forest edge (41)		Forest agricultural edge (38)		Suburban forest (30)		Pole stage forest (21)		Shrub/sapling stage forest (33)		ANCOVA <i>P</i>
	Mean	SE ^b	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Yellow-rumped Warbler (<i>D. coronata</i>) ^T	1.15	0.57	0.62	0.35	0.18	0.12	0.13	0.10	0.00	0.00	1.21	0.78	0.075
Black-throated Green Warbler (<i>D. virens</i>) ^N	1.31	0.20 ^B	2.17	0.30 ^A	0.89	0.16 ^B	0.63	0.17 ^B	0.62	0.22 ^B	1.00	0.22 ^B	<0.001
Blackburnian Warbler (<i>D. fusca</i>) ^N	0.48	0.10	0.77	0.18	0.34	0.12	0.30	0.15	0.14	0.10	0.45	0.15	0.105
Pine Warbler (<i>D. pinus</i>) ^T	0.17	0.08 ^A	0.40	0.14 ^A	0.13	0.09 ^A	0.03	0.03 ^A	0.00	0.00 ^A	0.61	0.22 ^A	0.011
Bay-breasted Warbler (<i>D. castaneata</i>) ^N	0.31	0.08	0.45	0.12	0.24	0.08	0.13	0.08	0.00	0.00	0.27	0.11	0.064
Blackpoll Warbler (<i>D. striata</i>) ^N	1.03	0.22	0.90	0.23	1.13	0.26	0.93	0.20	0.81	0.22	0.27	0.14	0.118
Black-and-white Warbler (<i>Mniotilta varia</i>) ^N	0.26	0.08	0.52	0.13	0.37	0.10	0.27	0.14	0.09	0.07	0.54	0.13	0.136
American Redstart (<i>Setophaga ruticilla</i>) ^N	0.28	0.09	0.62	0.16	0.53	0.18	0.43	0.14	0.09	0.09	0.73	0.18	0.095
Ovenbird (<i>Seiurus aurocapillus</i>) ^N	0.24	0.09	0.12	0.06	0.05	0.04	0.20	0.10	0.05	0.05	0.09	0.05	0.298
Wilson's Warbler (<i>Wilsonia pusilla</i>) ^N	0.00	0.00	0.15	0.09	0.08	0.06	0.03	0.03	0.00	0.00	0.15	0.08	0.210
Canada Warbler (<i>W. canadensis</i>) ^N	0.05	0.03	0.20	0.07	0.05	0.05	0.10	0.06	0.05	0.05	0.24	0.10	0.094
Scarlet Tanager (<i>Piranga olivacea</i>) ^N	0.41	0.10 ^A	0.60	0.19 ^A	0.68	0.20 ^A	0.20	0.09 ^A	0.00	0.00 ^A	0.24	0.09 ^A	0.032
Rose-breasted Grosbeak (<i>Phœnicurus ludovicianus</i>) ^N	0.15	0.08	0.22	0.18	0.24	0.12	0.07	0.05	0.00	0.00	0.09	0.05	0.524

^a N = Nearctic-Neotropical migrant, T = temperate migrant, R = resident/nonmigrant.

^b Column means with the same letter were not significantly different (pair-wise ANOVAs; experimentwise error rate controlled at $\alpha = 0.05$ using Bonferroni method).

TABLE 2. Species richness and abundance of migratory guilds within mixed species landbird flocks in six habitats in the Ridge and Valley Province of central Pennsylvania, fall 1998 and 1999. Flock sample sizes are in parentheses.

Variable	Forest interior (57)		Forest edge (41)		Forest agricultural edge (38)		Suburban forest (30)		Pole stage forest (21)		Shrub/sapling stage forest (33)		ANCOVA <i>P</i>
	Mean	SE ^b	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Nearctic-Neotropical migrant richness ^a	5.33	0.42 ^{AB}	7.46	0.64 ^A	6.60	0.58 ^A	4.97	0.41 ^{AB}	3.43	0.44 ^B	6.36	0.75 ^{AB}	0.001
Temperate migrant richness	1.44	0.22 ^A	1.37	0.20 ^{AB}	0.60	0.15 ^B	0.67	0.21 ^{AB}	0.43	0.20 ^B	1.18	0.20 ^{AB}	0.002
Resident richness	2.42	0.17 ^A	3.00	0.19 ^A	2.74	0.21 ^A	2.60	0.29 ^A	0.86	0.16 ^B	1.61	0.21 ^B	<0.001
Total richness	9.19	0.52 ^B	11.83	0.69 ^A	9.95	0.68 ^{AB}	8.23	0.57 ^B	4.71	0.44 ^C	9.15	0.89 ^B	<0.001
Nearctic-Neotropical migrant abundance	9.96	0.95 ^{AB}	18.51	3.85 ^A	11.63	1.54 ^{AB}	8.30	0.91 ^{ABC}	4.86	0.78 ^C	10.76	1.50 ^{BC}	<0.001
Temperate migrant abundance	4.33	1.04 ^A	3.27	0.67 ^A	0.79	0.19 ^B	1.23	0.45 ^{AB}	0.76	0.39 ^B	3.03	0.88 ^{AB}	<0.001
Resident abundance	5.70	0.53 ^{ABC}	7.19	0.56 ^A	6.26	0.50 ^{AB}	6.67	0.84 ^{AB}	3.09	0.63 ^C	4.42	0.63 ^{BC}	<0.001
Total abundance	23.03	1.90 ^B	33.63	4.46 ^A	20.60	1.73 ^B	17.43	1.64 ^B	8.95	1.04 ^C	20.64	2.38 ^B	<0.001

^a Richness = total number of species in each migratory guild; Abundance = total number of individuals in each migratory guild.
^b Habitat means with the same letter were not different (pair-wise ANOVAs; experiment-wise error rate controlled at $\alpha = 0.05$ using Bonferroni method).

consistently had the smallest and least diverse flocks.

Third, flock behavior suggested that food availability may have been higher in edge-dominated habitats than in other habitats. After accounting for variation in flock size, movement rates did vary among habitats, with flocks in edge-dominated habitats having low mean movement rates relative to flocks in pole stage forest and forest interior. While this suggests that food availability was greater in edge habitats, there were no pairwise differences ($P < 0.003$) among habitats after Bonferroni adjustment and sample size for flock movement rate was low in pole stage forests. Despite this, there is reason to expect that flocks in edge habitats would experience higher food availability because arthropods often are more abundant at forest edges than in forest interior (Helle and Muona 1985, Bedford and Usher 1994, Jokimäki et al. 1998).

Forest edges may have had high abundance and diversity of migrants simply because birds accumulate at edges. Studies of Black-capped Chickadee flocks during winter have reported that forest edges are used more frequently than forest interior because edges act as conduits and channel flock movement (Desrochers and Fortin 2000). Indeed, in our study flocks in edge-dominated habitats often remained close to edges throughout observation periods. However, these flocks often moved only short distances and had low movement rates relative to most interior habitats (pole stage and forest interior), and not the higher movement rates that would be expected if edges functioned primarily as channels of flock movement. In addition, high arthropod abundance at forest edges would be an important incentive for flock members to actively forage at edges. While the possibility exists that forest edges functioned, in part, as conduits to flock movement in our study, our observations suggest this was less important in explaining habitat use patterns of mixed species flocks during fall.

Several features of edge habitats may have contributed to their high use by migrants. In addition to higher invertebrate abundance, forest edges often have greater stem densities and structural diversity (Gysel 1951), higher fruit abundance (Blake and Hoppes 1986, Rodewald 2001), and presence of tall herbaceous

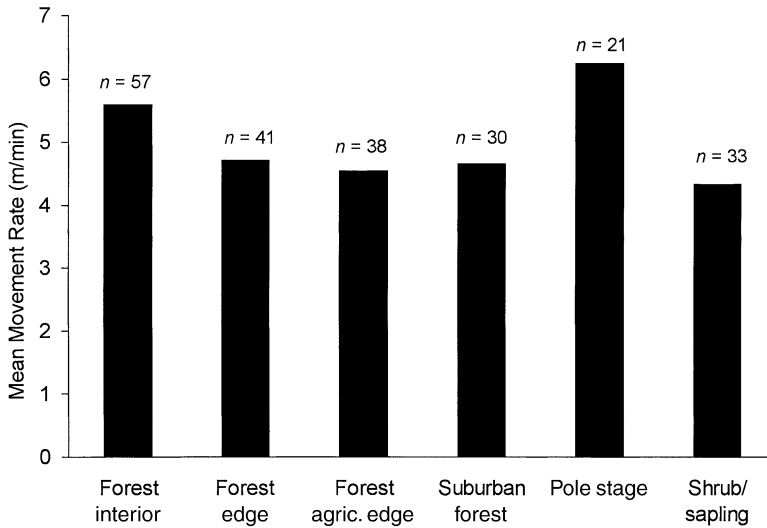


FIG. 1. Mean movement rate of mixed species landbird flocks in six forest habitats in the Ridge and Valley Province of central Pennsylvania during fall 1998 and 1999. Column means were not statistically different ($P > 0.003$) in pairwise comparisons (Bonferroni adjusted).

vegetation during late summer and fall. We observed that patterns of migrant abundance and richness seemed to be positively associated with habitat heterogeneity at edges. For example, pole stage forests, where there was little midstory and understory vegetation, had consistently low species richness and abundance of birds within mixed species flocks; pole stage forests have similar patterns of avian species richness and abundance during the breeding season (Conner and Adkisson 1975, DeGraff and Chadwick 1987). Also, forest agricultural edge habitat usually had notably lower density of shrubs and saplings compared to forest edge habitat, and this could explain differences in migrant abundance and richness between these two habitats. While little research has specifically examined habitat use by mixed species flocks during migration, several studies have reported relationships between habitat characteristics and migrant abundance and species richness. For example, heterogeneous vegetation of scrub/shrub and pine forest habitats on Gulf coast islands of Mississippi had higher abundance and species richness of spring migrants than less heterogeneous vegetation in primary dune and marsh/meadow habitats (Moore et al. 1990). In addition, foliage density was positively correlated with abundance of spring and fall mi-

grant songbirds within forest tree fall gaps (Blake and Hoppes 1986, Martin and Karr 1986), and may provide denser protective cover, allowing migrants to lower their predation risk (Morse 1973, Grubb and Greenwald 1982).

Frugivory is frequent in many species of Nearctic-Neotropical migrant landbirds during migration (Parrish 2000). While some studies have suggested that fruit plays a minor role in lipid deposition in migratory birds (Berthold 1976, Izhaki and Safriel 1989), recent evidence suggests that fruit is far more important in promoting lipogenesis in some migrant species (Bairlein 1990, Parrish 1997). We observed individuals of a number of species that followed mixed species flocks consuming fruit, but flock members were largely insectivorous and flocks tended not to linger in fruiting plants. However, exceptions occurred when some species (e.g., Red-eyed Vireo and Rose-breasted Grosbeak) joined flocks of frugivorous birds (e.g., Cedar Waxwing, *Bombicilla cedrorum*, and American Robin, *Turdus migratorius*) and, in that situation, consumed fruit more readily. Overall, though, we do not believe that fruit resources at habitat edges were of primary importance in the selection of habitats by mixed species flocks we examined.

We regularly observed mixed species flocks of migrants foraging in areas with tall, dense herbaceous vegetation, such as mixed goldenrods (*Solidago* spp.), asters (*Aster* spp.), grasses (Poaceae), and corn (*Zea*). This vegetation occurred frequently within forest edge, forest agricultural edge, and shrub/sapling stage habitats during fall. Use of herbaceous nonfruiting vegetation by fall Nearctic-Neotropical migrants has been only anecdotally reported from eastern North America, but this behavior is not unusual during fall migration, especially for certain species of wood warblers (Dunn and Garrett 1997; PGR and MCB unpubl. data).

Mixed species flocks may have been attracted to edges for other reasons. Flocks that occurred in edge-dominated habitats during fall foraged closest to edges earlier in the day. This suggests that attraction to forest edges during morning may have been partly related to warmer temperatures at edges exposed to sunlight (Huertas and Diaz 2001) or higher light levels at edges than in adjacent forest. However, we regularly observed flocks during the afternoon within edge-dominated habitats when edges were not exposed to sunlight and on days with overcast skies.

The presence of parids in flocks may have attracted migrating birds as well. Moore and Aborn (2000) suggested that individual migrants may use parids and/or mixed species flocks as a selection cue for high quality habitat with higher resource availability. Joining flocks that contain residents during *en route* periods may be especially important for migrant landbirds because they typically are unfamiliar with local habitat and resource availability, having often arrived at a new stopover location during the previous night. Sampling habitats requires time, and migration is a time-limited period for migrants (Alerstam and Lindström 1990). Migrants that join flocks may benefit by increasing their foraging efficiency (Krebs et al. 1972) and lowering their risk of predation (Hamilton 1971, Morse 1980). Parids were present in over 80% of mixed species flocks and frequently were observed leading these flocks to new areas. Coupled with the fact that relatively few individuals of species that joined mixed species flocks were encountered outside flocks, it

seems possible that parid occurrence influenced the habitat use of migrants.

Forest edges and structurally heterogeneous habitats seem to provide high quality fall habitat for many migratory landbirds during a critical period in their annual life cycles. While forest edge habitats are not considered high quality nesting habitat for many species of forest landbirds due to negative edge effects (Chasko and Gates 1982, Askins et al. 1987), they do seem to provide important resources for many species during migration. In addition, habitats with dense vegetation, including forest edges, have been shown to be important postbreeding (premigration) habitat for forest-breeding juvenile (Vega Rivera et al. 1998) and adult (Vega Rivera et al. 1999) Wood Thrushes (*Hylocichla mustelina*). Thus, effort should be made to improve and/or maintain existing edge habitat in certain local situations. Permanent and temporary anthropogenic edge habitats associated with suburban and agricultural woodlots, treerows in agricultural fields, forest cutting operations, power line right-of-ways, rural roads, and highways are examples of locations where land managers or private landowners could manage for heterogeneous habitat. However, because breeding season habitat requirements of migratory birds also must be considered, conservation benefits of local actions can be maximized only if developed within a regional context (Petit 2000). For example, maintenance or creation of edges to provide habitat for migrating landbirds may be inappropriate in large, contiguous forests given potential negative effects of edges on breeding landbirds. Ultimately, a better understanding of *en route* habitat relationships of migratory landbirds is needed to develop comprehensive conservation plans for these birds.

ACKNOWLEDGMENTS

R. A. Askins, A. D. Rodewald, R. H. Yahner, and anonymous reviewers made suggestions to improve the manuscript. We thank A. Siepielski, G. M. Forcey, J. Mollenauer, and S. J. Rapasky for their assistance with field observations of mixed species bird flocks and data entry. We thank private landowners, Centre Region Parks and Recreation Dept., Pennsylvania Bureau of Forestry, and Pennsylvania Game Comm. for access to study habitats. For financial support we thank Pennsylvania's Wild Resource Conservation Fund, the School of Forest Resources at The Pennsylvania State

Univ., and the Wilson Ornithological Society and Cooper Ornithological Society for student research awards.

LITERATURE CITED

- ALERSTAM, T. AND A. LINDSTRÖM. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pp. 331–351 in *Bird migration: physiology and ecophysiology* (E. Gwinner, Ed.). Springer-Verlag, Berlin, Germany.
- AMERICAN ORNITHOLOGISTS' UNION. 1998. Check-list of North American birds, 7th ed. American Ornithologists' Union, Washington, D.C.
- ASKINS, R. A., M. J. PHILBRICK, AND D. S. SUGENO. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biol. Conserv.* 39:129–152.
- BAIRLEIN, F. 1990. Nutrition and food selection in migratory birds. Pp. 198–213 in *Bird migration: physiology and ecophysiology* (E. Gwinner, Ed.). Springer-Verlag, Berlin, Germany.
- BEDFORD, S. E. AND M. B. USHER. 1994. Distribution of arthropod species across the margins of farm woodlands. *Agric. Ecosyst. Environ.* 48:295–305.
- BERTHOLD, P. 1976. The control and significance of animal and vegetable nutrition in omnivorous songbirds. *Ardea* 64:140–154.
- BLAKE, J. G. AND W. G. HOPPES. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk* 103:328–340.
- CHASKO, G. G. AND J. E. GATES. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildl. Monogr.* 82:1–41.
- CONNER, R. N. AND C. S. ADKISSON. 1975. Effects of clearcutting on the diversity of breeding birds. *J. For.* 73:781–785.
- DEGRAFF, R. M. AND N. L. CHADWICK. 1987. Forest type, timber class, and New England breeding birds. *J. Wildl. Manage.* 51:212–217.
- DEGRAFF, R. M. AND J. H. RAPPOLE. 1995. Neotropical migratory birds: natural history, distribution, and population change. Cornell Univ. Press, Ithaca, New York.
- DESROCHERS, A. AND M.-J. FORTIN. 2000. Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. *Oikos* 91:376–384.
- DUNN, J. L. AND K. L. GARRETT. 1997. A field guide to warblers of North America. Houghton Mifflin Co., Boston, Massachusetts.
- GRUBB, T. C., JR. AND L. GREENWALD. 1982. Sparrows and a brushpile: foraging response to different combinations of predation risk and energy cost. *Anim. Behav.* 32:120–131.
- GYSEL, W. L. 1951. Borders and openings of beech-maple woodlands in southern Michigan. *J. For.* 49:13–19.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31:295–311.
- HELLE, P. AND J. MUONA. 1985. Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. *Silva Fenn.* 19:281–294.
- HUERTAS, D. L. AND J. A. DIAZ. 2001. Winter habitat selection by a montane forest bird assemblage: the effects of solar radiation. *Can. J. Zool.* 79:279–284.
- HUTTO, R. L. 1985. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? *Auk* 102:120–132.
- HUTTO, R. L. 1987. A description of mixed species insectivorous bird flocks in western Mexico. *Condor* 89:282–292.
- HUTTO, R. L. 1990. Measuring the availability of food resources. *Stud. Avian Biol.* 13:20–28.
- IZHAKI, I. AND U. N. SAFRIEL. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54:23–32.
- JOKIMÄKI, J., E. HUHTA, J. ITÄMIES, AND P. RAHKO. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Can. J. For. Res.* 28:1068–1072.
- KEAST, A. 1980. Migratory Parulidae: what can species co-occurrence in the north reveal about ecological plasticity and wintering patterns? Pp. 457–476 in *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (A. Keast and E. S. Morton, Eds.). Smithsonian Inst. Press, Washington, D.C.
- KREBS, J. R., M. H. MACROBERTS, AND J. M. CULLEN. 1972. Flocking and feeding in the Great Tit *Parus major*—an experimental study. *Ibis* 114:507–530.
- LOVETTE, I. J. AND R. T. HOLMES. 1995. Foraging behavior of American Redstarts in breeding and wintering habitats: implications for relative food availability. *Condor* 97:782–791.
- MARTIN, T. E. 1985. Selection of second-growth woodlands by frugivorous migrating birds in Panama: an effect of fruit size and plant density. *J. Trop. Ecol.* 1:157–170.
- MARTIN, T. E. AND J. R. KARR. 1986. Patch utilization by migrating birds: resource oriented? *Ornis Scand.* 17:165–174.
- MOORE, F. R. AND D. A. ABORN. 2000. Mechanisms of *en-route* habitat selection: how do migrants make habitat decisions during stopover? *Stud. Avian Biol.* 20:34–42.
- MOORE, F. R., S. A. GAUTHREAUX, JR., P. KERLINGER, AND T. R. SIMONS. 1995. Habitat requirements during migration: important link in conservation. Pp. 121–144 in *Ecology and management of Neotropical migratory birds* (T. E. Martin and D. M. Finch, Eds.). Oxford Univ. Press, New York.
- MOORE, F. R., P. KERLINGER, AND T. R. SIMONS. 1990. Stopover on a Gulf Coast barrier island by spring trans-Gulf migrants. *Wilson Bull.* 102:487–500.
- MORSE, D. H. 1970. Ecological aspects of some mixed species foraging flocks of birds. *Ecol. Monogr.* 40:119–168.
- MORSE, D. H. 1973. Interaction between tit flocks and Sparrowhawks *Accipiter nisus*. *Ibis* 115:591–593.

- MORSE, D. H. 1980. Behavioral mechanisms in ecology. Harvard Univ. Press, Cambridge, Massachusetts.
- MORSE, D. H. 1989. American warblers: an ecological and behavioral perspective. Harvard Univ. Press, Cambridge, Massachusetts.
- PARRISH, J. D. 1997. Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. *Condor* 99:681–697.
- PARRISH, J. D. 2000. Behavioral, energetic, and conservation implications of foraging plasticity during migration. *Stud. Avian Biol.* 20:53–70.
- PETTIT, D. R. 2000. Habitat use by landbirds along Nearctic-Neotropical migration routes: implications for conservation of stopover habitats. *Stud. Avian Biol.* 20:15–33.
- POOLE, A. AND F. GILL (Eds.). 1993–2001. The birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, the American Ornithologists' Union, Washington, D.C., and The Birds of North America, Inc., Philadelphia, Pennsylvania.
- ROBINSON, S. K. AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918–1931.
- RODEWALD, P. G. 2001. Ecology and behavior of migratory songbirds during stopover periods. Ph.D. diss., The Pennsylvania State Univ., University Park.
- SAS INSTITUTE, INC. 1990. SAS/STAT user's guide, ver. 6, 4th ed. SAS Inst., Cary, North Carolina.
- SUTHERS, H. B., J. M. BICKAL, AND P. G. RODEWALD. 2000. Use of successional habitat and fruit resources by songbirds during autumn migration in central New Jersey. *Wilson Bull.* 112:249–260.
- VEGA RIVERA, J. H., J. H. RAPPOLE, W. J. MCSHEA, AND C. A. HAAS. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. *Condor* 100:69–78.
- VEGA RIVERA, J. H., W. J. MCSHEA, J. H. RAPPOLE, AND C. A. HAAS. 1999. Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. *Auk* 116:458–466.
- YONG, W., D. M. FINCH, F. R. MOORE, AND J. E. KELLY. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. *Auk* 115:829–842.

APPENDIX. Landbird species that infrequently attended mixed species flocks in the Ridge and Valley Province of central Pennsylvania, fall 1998 and 1999. Sample sizes were insufficient to permit statistical analyses.

Yellow-billed Cuckoo (*Coccyzus americanus*)
 Yellow-bellied Flycatcher (*Empidonax flaviventris*)
 Least Flycatcher (*E. minimus*)
 Great Crested Flycatcher (*Myiarchus crinitus*)
 Eastern Phoebe (*Sayornis phoebe*)
 Yellow-throated Vireo (*Vireo flavifrons*)
 Warbling Vireo (*V. gilvus*)
 Red-breasted Nuthatch (*Sitta canadensis*)
 Winter Wren (*Troglodytes troglodytes*)
 Northern Parula (*Parula americana*)
 Blue-winged Warbler (*Vermivora pinus*)
 Golden-winged Warbler (*V. chrysoptera*)
 Orange-crowned Warbler (*V. celata*)
 Yellow Warbler (*Dendroica petechia*)
 Yellow-throated Warbler (*D. dominica*)
 Prairie Warbler (*D. discolor*)
 Palm Warbler (*D. palmarum*)
 Cerulean Warbler (*D. cerulea*)
 Worm-eating Warbler (*Helmitheros vermivorus*)
 Connecticut Warbler (*Oporornis agilis*)
 Mourning Warbler (*O. philadelphia*)
 Hooded Warbler (*Wilsonia citrina*)
 Common Yellowthroat (*Geothlypis trichas*)
 Chipping Sparrow (*Spizella passerina*)
 Dark-eyed Junco (*Junco hyemalis*)
 Baltimore Oriole (*Icterus galbula*)
