A COMPARISON OF SHRUB-DOMINATED AND FORESTED HABITAT USE BY SPRING MIGRATING LANDBIRDS IN NORTHEASTERN PENNSYLVANIA

Robert J. Smith^{1,3} and Margret I. Hatch²

¹Department of Biology, The University of Scranton, Scranton, PA 18510 ²Penn State Worthington Scranton, 120 Ridge View Drive, Dunmore, PA 18512

Abstract. Long-term datasets reveal declines in many populations of landbird migrants, with declines especially evident in shrub-nesting species. Moreover, transitional shrub-dominated habitats are becoming scarce, reducing breeding habitat for these species. Because migrants often occupy habitats en route similar to those used in the breeding season, the persistence of shrub-dominated habitats may be especially critical for these species during passage. Because little is known about migrant-habitat relationships, especially at inland, unforested stopover sites, we compared the importance of forested and upland shrub-dominated habitat to spring migrating landbirds by comparing; (1) temporal and habitat-related variation in resource abundance, and (2) migrant use of forested vs. shrub-dominated habitat during stopover. We collected data on bird-habitat relationships and invertebrate abundance from both habitats at two sites in or near Lackawanna State Park, Lackawanna County, Pennsylvania. We captured and counted more short-distance and long-distance migrants in shrub habitat (256 birds per 1000 mist-net hours and seven birds per 100 m of survey transect) than in forested habitat (67 birds per 1000 mist-net hours and three birds per 100 m of transect), and shrub habitat contained a somewhat greater diversity of migrants (H' = 4.0 vs. 3.9). We also measured greater flying invertebrate biomass in shrub vs. forested habitat, although there was no difference in flightless invertebrate biomass between the two habitats. Our results support the hypothesis that migrant habitat use reflects spatial differences in resource abundance and indicate that shrubdominated habitats may be important stopover habitat for landbird migrants.

Key words: habitat use, landbird, resources, spring migration, stopover.

Comparación en el Uso de Arbustales y Bosque por Aves Migratorias de Primavera en el Noreste de Pensilvania

Resumen. Las bases de datos de largo plazo revelan disminuciones en muchas de las poblaciones de aves terrestres migratorias, con disminuciones especialmente evidentes en especies que nidifican en ambientes arbustivos. Además, los hábitats de transición dominados por arbustos se están tornando escasos, lo que reduce el hábitat reproductivo para estas especies. Debido a que generalmente los hábitats que las aves migratorias utilizan durante sus rutas migratorias son similares a los que utilizan en la época reproductiva, la persistencia de arbustales puede ser especialmente crucial para estas especies durante los desplazamientos migratorios. Debido a que se conoce poco sobre las relaciones entre las aves migratorias y sus hábitats, especialmente en sitios de parada deforestados localizados tierra adentro, comparamos la importancia de hábitats de bosque y arbustales para aves terrestres migratorias de primavera con relación a: (1) abundancia de recursos asociada a variación temporal y de hábitat y (2) utilización por las aves migratorias de los hábitats de bosque vs. arbustales. Colectamos datos sobre la relación entre hábitats y aves, y sobre la abundancia de invertebrados en los dos hábitats estudiados en dos sitios, dentro o cerca del Parque Estadual Lackawanna, condado de Lackawanna, Pensilvania. Capturamos y contamos más aves migratorias de distancias cortas y largas en el arbustal (256 aves por 1000 horas de red de neblina y siete aves por 100 m de transecto muestreado) que en el hábitat de bosque (67 aves por 1000 horas de red y tres aves por 100 m de transecto). El arbustal tuvo una diversidad un poco mayor de aves migratorias (H' = 4.0 vs. 3.9). También medimos una mayor biomasa de invertebrados voladores en el arbustal que en el bosque, a pesar de que no hubo diferencia en la biomasa de invertebrados no voladores entre los dos hábitats. Nuestros resultados apoyan la hipótesis de que el uso de hábitat durante la migración refleja las diferencias espaciales en la abundancia de recursos e indican que los hábitats dominados por arbustos pueden ser sitios de parada importantes para las aves terrestres migratorias.

INTRODUCTION

Long-term datasets reveal population declines in many migrant landbird species (Robbins et al. 1989, Askins et al. 1990). Declines are especially evident in shrub-nesting species, as revealed by records collected at banding stations and bird observatories during migration (Askins 2000). Further, transitional shrub-dominated habitats are becoming scarce, reducing breeding habitat for these species (Askins 2000, Oehler 2003). Because migrating landbirds are thought to reference innate

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information about breeding habitat when making decisions about habitat use during migration, i.e., migrants tend to occupy habitats en route that are similar to those used in the breeding season (Moore and Aborn 2000), the persistence of shrub-dominated habitats may be critical for these species during passage.

Although the debate over causes of migrant population declines continues, increasing evidence suggests that the migratory period may play an important role in population limitation (Moore et al. 1995, Sherry and Holmes 1995). Indeed, recent work by Sillett and Holmes (2002) suggests that mortality rates for songbird migrants may be up to 15 times higher during migration than in the other, stationary periods of the avian annual cycle. Because migrants cannot fly nonstop between wintering and breeding areas (Blem 1980), they must periodically stop to rest and refuel prior to continuing migration. Consequently, the extent to which a migrant landbird is able to locate suitable stopover habitat to satisfy energetic demands and meet other en route exigencies (Moore et al. 1995, 2005, Mehlman et al. 2005) determines whether it successfully completes migration. Moreover, as recent work suggests, arrival at the destination in a timely manner and in superior condition may have fitness consequences (Sandberg 1996, Sandberg and Moore 1996, Smith and Moore 2005).

Until recently, attention has mainly focused on events associated with the breeding and wintering phases of the annual cycle (Sherry and Holmes 1995). As a result, the importance of stopover habitat has been largely overlooked in the development of conservation strategies (Moore et al. 1995, Hutto 2000). Even with the recent interest in the en route ecology of songbirds both in eastern (Moore 2000, Rodewald and Matthews 2005, Smith et al. 2007) and western (Swanson et al. 2003, Carlisle et al. 2004) North America, there remains a need for basic information describing the ecology of migrants during passage. We need to develop a better understanding of what types of habitat are important, where those habitats occur, what makes them important, and how their distribution and abundance are changing as a result of development and land conversion (Moore et al. 1995, 2005, Mehlman et al. 2005). If persistence of migrant populations depends on locating favorable habitat throughout the annual cycle, factors associated with en route ecology of migrants must figure prominently in any analysis of population change and in the development of a comprehensive conservation plan for migrant species (Moore et al. 1995). Unless habitat requirements during migration are met, conservation measures focused on temperate breeding grounds or Neotropical wintering areas will be compromised (Moore and Simons 1992).

Our objective was to determine whether migrant landbird diversity and abundance differed between forested and shrubdominated stopover habitat and whether migrant use of these habitats was associated with resource (invertebrate) abundance. To answer these questions we used an integrated approach, combining capture data from two bird banding stations with avian survey and resource abundance data to evaluate the relative importance of forested and shrub-dominated habitat to songbirds migrating through northeastern Pennsylvania.

METHODS

We collected data describing bird-habitat relationships concurrently from forested and upland shrub-dominated habitats in Lackawanna County, northeastern Pennsylvania, during the spring migratory periods of 2005–2007. Elevation at our sites ranged from 305 to 360 m. We surveyed and captured birds from the third week of April through 14 June. We used 14 June to mark the endpoint of spring migration because both historical records (McWilliams and Brauning 2000) and our capture data (RJS and MIH, unpubl. data) indicate that many species, including those that breed north of our study area (e.g., Tennessee Warbler [*Vermivora peregrine*], Rubycrowned Kinglet [*Regulus calendula*], and Swainson's Thrush [*Catharus ustulatus*]), occur in Pennsylvania in nonbreeding habitats through the second week of June.

We monitored both forested and shrub-dominated habitats at two sites: Lackawanna State Park, and private lands (hereafter referred to as the Bushko site) immediately adjacent to the park. Forested habitats were predominately upland, dominated by red maple (Acer rubrum), sugar maple (A. saccharum), ash (Fraxinus spp.), and black cherry (Prunus serotina), with eastern hemlock (Tsuga canadensis) occurring in moister areas. Shrub-dominated habitat chosen for this work was approximately 25-30 years postagriculture and was a mix of exotic (primarily honeysuckle [Lonicera tartarica]) and native shrubs (primarily dogwood [Cornus spp.] and arrowwood viburnum [Viburnum dentatum]) as well as a small number of saplings of most tree species found in the forested habitat. The dominant shrub was honeysuckle, which comprised 41% of shrub and sapling stems in shrub-dominated habitat and 23% of stems in forested habitat. Honeysuckle completed leaf development some 13.0 ± 0.6 days prior to 15 May, whereas the phenology of other species common to our site was a week or more delayed relative to honeysuckle (RJS and MIH, pers. obs.). Therefore, we created an early migration period subset of our data, analyzing only samples through 15 May, to examine the potential influence of this early leaf development.

INVERTEBRATES

All invertebrate sampling took place within the two mist-netting locations (the Bushko site or the Lackawanna State Park site). To estimate flying arthropod abundance, we placed Malaise traps at four permanent sampling locations, one in each habitat type at both sites. Traps were cleared of invertebrates every three days. Samples were preserved in 70% ethanol and later dried to a constant mass at 70°C. We corrected for differences in trapping time by dividing dried biomass by total trapping time (in minutes) and multiplying by 100.

We also collected grab samples of each common tree or shrub species to estimate relative abundance of flightless arthropods found on branches and leaves, hereafter referred to as "substrate invertebrates," in both habitats (Cooper and Whitmore 1990). At both sites and for each sampling round we collected samples from four randomly chosen locations in each habitat for a total of 16 samples (eight shrub and eight forested samples per sampling round) every six days. Samples were collected by placing a bag over a branch, sealing the bag, clipping the branch, and fumigating the bag contents. All invertebrates were sorted to size and taxonomic Order. We used the equations of Hódar (1996) to estimate arthropod biomass for each group. To correct for differences in the amount of vegetation collected among samples, we weighed clipped branches and report results as milligrams of invertebrate biomass per 100 grams of vegetation.

BIRD SURVEYS

We surveyed migrants daily between sunrise and 09:30 using strip transects ranging from 150 to 300 m in length. Transect locations were selected to maintain within-habitat age, vegetation composition, and vegetation characteristics (Table 1) as much as possible. We alternated surveys between habitats, i.e., following a survey in one habitat type we subsequently counted birds in the other habitat. Each survey consisted of slowly walking the transect line and recording species, number of individuals, and sex for all birds heard or seen within 25 m of either side of the transect centerline. Because we were interested in habitat use, we excluded from our analyses all birds merely seen flying over the transect. To account for differences in transect length, we divided detections by transect length and multiplied by 100, reporting results as detections per 100 m of transect.

MIST-NETTING

We had two banding sites (Lackawanna and Bushko) and captured migrants using mist nets in forested (n = 22) and shrubdominated (n = 25) habitats. Both sites (Lackawanna ~10 ha,

TABLE 1. Mean \pm SE habitat characteristics of forest and shrub used by spring migrants, measured within 87 0.04 ha circular plots at sites within and adjacent to Lackawanna State Park, Lackawanna County, Pennsylvania, 2007.

Vegetation metrics	Forested habitat $(n = 44)$	Shrub-dominated habitat $(n = 43)$
Average tree diameter at		
breast height (cm)	99.9 ± 6.7	25.4 ± 3.0
Percent ground cover	39 ± 8	64 ± 5
Percent canopy cover	75 ± 5	14 ± 4
Canopy height (m)	22.8 ± 2.7	$13.0\pm0.6^{\mathrm{a}}$
Shrub height (m)	3.8 ± 0.6	3.2 ± 0.2
Shrub and sapling stem density (stems per ha) ^b	1890	8976

^aShrub-dominated habitat did not have a continuous canopy, but did have scattered emergent trees.

^bEstimated stem density for the 10 most common shrub and tree saplings.

Bushko ~ 6 ha) were within the larger survey area (~ 1259 ha). Straight-line distance between the two sites was 3.2 km. Mistnetting locations were selected to maintain within-habitat age, vegetation composition, and vegetation characteristics (Table 1) as much as possible. Nets were located >50 m from the edge of each habitat. Forest nets included a series of 'high' nets, in which one net was positioned on top of another, so that the top net was elevated to a height of approximately 8 m. At each site, nets were opened shortly before sunrise and remained open through the early afternoon, and were checked at 30 min intervals. We closed nets if temperatures dropped below 3°C, or in the event of high wind or rain. For each individual captured we recorded: capture date and time, species, age and sex where possible (Pyle 1997), mass, and tarsus length. All captured birds were banded with a U.S. Geological Service aluminum leg band. All recaptures were measured without reference to previous records.

STATISTICAL ANALYSES

Invertebrates. We used a square-root transformation to bring Malaise trap data into compliance with testing assumptions (Tabachnick and Fidell 1996). We then used a general linear model (GLM) to assess the influence of year, site, and habitat type (shrub vs. forest) on biomass. Because transformations did not normalize our grab sample data, we performed a GLM on ranks to assess the influence of year, site, sample week, and habitat type on substrate invertebrate abundance. We executed additional GLMs on ranked data followed by Tukey's post-hoc tests (Zar 1996) to examine relationships between substrate arthropods and vegetation type. We used Mann-Whitney *U*-tests to compare total substrate arthropod biomass estimates by habitat throughout the entire spring migration period and in the early migration period. We report means \pm SE.

Birds. We categorized species as long-distance migrants (species wintering predominately south of the Tropic of Cancer) or short-distance migrants (species wintering predominately in the temperate zone; DeGraaf and Rappole 1995, Carlisle et al. 2004; see Appendix for a full list of study species and migratory distance classifications). We included the Blue-headed Vireo (*Vireo solitarius*), Ruby-crowned Kinglet, and Yellow-rumped Warbler (*Dendroica coronata*) in our short-distance category (Ingold and Wallace 1994, American Ornithologists' Union 1998, Hunt and Flaspohler 1998, James 1998). We excluded Ruby-throated Hummingbirds (*Archilochus colubris*) from our survey dataset because we did not collect capture data for this species.

We used a GLM on our capture data to assess the influence of year, site, and habitat type on abundance of short-distance and long-distance migrants. We used a GLM on ranks for our survey data because transformations did not normalize these data. We made species-level comparisons of habitat use for both capture and survey data. To make these comparisons, we calculated chi-square values using data that had been corrected for differential sampling effort (Carlisle et al. 2004). We only made statistical comparisons for species with total detections or captures exceeding 24, so that expected cell frequencies were ≥ 5 (Brower et al. 1990). Because of the number of species involved, we made many pairwise comparisons, which increases the probability of making a Type I error (Moran 2003). However, there are mathematical, logical, and practical objections to adjusting *P*-values for tables of multiple statistical tests (Moran 2003). Therefore, we present effect magnitudes and uncorrected *P*-values, and reiterate Moran's (2003) point that while one significant effect in a large table of multiple statistical tests might be of concern, a high proportion of significant species-level results are strong evidence against the null hypothesis.

Diversity indices. To estimate species diversity and make comparisons between forested and shrub-dominated sites, we calculated Shannon diversity indices (Magurran 1988) for each habitat type using both our banding and survey data. The Shannon diversity index, which is based on proportional species abundance (Magurran 1988), is a widely used metric for quantifying both species richness and abundance. In addition, use of this measure permits statistical comparisons between habitat types using a *t*-test (Magurran 1988). We used individual species detections per 100 m of transect as our metric to calculate H' for our survey data. Similarly, we used capture data that had been corrected for differences in capture time between habitats (individual species captured per 1000 mistnet hours) to calculate diversity.

Comparing mist-netting and survey data. We adjusted totals from each survey method by converting number of individuals for each species to a standard score using the following equation (Zar 1996, Carlisle et al. 2004):

$$Z = \frac{X_i - \mu}{\sigma},$$

where X_i = the total number of individuals of a given species, μ = the mean of species totals of all species, and σ = the standard deviation of the species total. We then used nonparametric correlations to look for associations between our capture and survey data.

RESULTS

INVERTEBRATE BIOMASS

Flying invertebrates (Malaise traps). There was no difference between study sites in biomass estimates derived from Malaise sampling ($F_{2,127} = 2.7$, P = 0.10), but there was a year effect ($F_{2,127} = 12.2$, P < 0.001), a habitat effect ($F_{2,127} = 12.6$, P = 0.001), and a significant interaction between year and habitat ($F_{2,127} = 7.6$, P = 0.001). We captured more flying insects in shrub habitats than in forested habitats in two of the three years of this study (Fig. 1).

Substrate invertebrates (Grab sampling). A GLM on ranks indicated that there was a year ($F_{2,1750} = 32.8, P < 0.001$;



FIGURE 1. Flying arthropod abundance in shrub-dominated and forested habitat in or near Lackawanna State Park, Lackawanna County, Pennsylvania, as estimated by Malaise trap sampling during spring migration in 2005–2007. Numbers above error bars indicate the number of samples collected; whiskers represent one standard error. The habitat effect was significant in 2005 and 2006, with more flying arthropods collected in shrub-dominated than in forested habitat.

greater biomass in 2005 and 2006 than in 2007) and sampling week ($F_{8,1750} = 5.7$, P < 0.001; average biomass increased with week) effect on biomass. There was not, however, a study site effect ($F_{1,1750} = 0.1$, P = 0.80), nor was there a shrub vs. forest effect ($F_{1,1750} < 0.1$, P = 0.95). Results of our grab sampling suggested that, over the course of the entire spring migration period, there was no difference between shrub and forested habitats in biomass of substrate invertebrates. During the early migration period, however, there appeared to be more total arthropod biomass in shrub-dominated habitat than in forested habitat (Z = 1.9, n = 377, P = 0.05; 3.4 ± 0.8 mg per 100 g vegetation in shrub, 1.7 ± 0.3 mg per 100 g vegetation in forest).

We also examined relationships between habitat and abundance of lepidopteran larvae, the predominant leaf-chewing arthropod group at our study site. We found no difference between forested and shrub-dominated habitat in larvae biomass throughout the entire migration period (Z = 0.7, n = 418, P =0.50; forest: 8.7 ± 1.5 mg per 100 g vegetation; shrub: 5.7 ± 0.8 mg per 100 g vegetation). Further comparison of lepidopteran larvae biomass by habitat during the early migration period, when leaf development of honeysuckle was advanced relative to other tree and shrub species, also indicated no significant difference (Z = 1.6, n = 87, P = 0.12; forest: 1.7 ± 0.3 mg per 100 g vegetation; shrub: 5.3 ± 1.2 mg per 100 g vegetation), though statistical testing power was low ($\beta = 0.05$).

When we examined the relationships between invertebrate abundance and the woody vegetation common to our study

	Ash	Black cherry	Dogwood	Hawthorn	Honeysuckle	Red maple	Sugar maple	Viburnum
Ash (Fraxinus spp.)		P = 1.0	P = 0.3	$P < 0.001^{\dagger}$	P = 0.03	P = 0.1	P = 1.0	$P = 0.01^{\dagger}$
Black cherry (Prunus	P = 1.0		P = 0.3	$P < 0.001^{\dagger}$	P = 0.02	$P = 0.03^{\dagger}$	P = 1.0	$P = 0.001^{\dagger}$
Dogwood (Cornus spp.)	P = 0.3	P = 0.3	1 010	$P < 0.001^{\dagger}$	P = 0.98	$P < 0.001^{\dagger}$	P = 0.5	$P < 0.001^{\dagger}$
Hawthorn (<i>Crataegus spp.</i>)	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001		<i>P</i> < 0.001	$P = 0.03^{\dagger}$	<i>P</i> < 0.001	P = 0.10
Honeysuckle (Lonicera								
tartarica)	$P = 0.03^{\dagger}$	$P = 0.02^{\dagger}$	P = 0.98	$P < 0.001^{\dagger}$		$P < 0.001^{\dagger}$	P = 0.06	$P < 0.001^{\dagger}$
Red maple (Acer rubrum)	P = 0.1	P = 0.03	P < 0.001	P = 0.03	P < 0.001		P = 0.003	P = 1.0
Sugar maple (Acer								
saccharum)	P = 1.0	P = 1.0	P = 0.5	$P < 0.001^{\dagger}$	P = 0.06	$P = 0.003^{\dagger}$		$P < 0.001^{\dagger}$
Arrowwood viburnum								
(Viburnum dentatum)	P = 0.01	P = 0.001	P < 0.001	P = 0.1	P < 0.001	P = 1.0	P < 0.001	

TABLE 2. Results of Tukey post-hoc tests comparing flightless invertebrate biomass between species of woody vegetation common to forested and shrub-dominated habitat at field sites in or adjacent to Lackawanna State Park, Lackawanna County, Pennsylvania. Invertebrates were collected by grab sampling in 2005, 2006, and 2007. A[†] indicates the species listed in the top row had significantly higher invertebrate biomass than the species in the left-hand column.

area, after controlling for year ($F_{2,1287}$ =6.5, P=0.002) and sample week ($F_{8,1287}$ =3.4, P=0.001), there was an effect of vegetation type on biomass ($F_{7,1287}$ =3.2, P=0.002). We obtained more invertebrate biomass in red maple, hawthorn, and *Viburnum* than in most other species, whereas honeysuckle contained less invertebrate biomass than most other species (Table 2, Fig. 2). Restricting the analysis to just shrubs common to our site



FIGURE 2. Flightless arthropod abundance by common vegetation species in shrub-dominated and forested habitat in or near Lackawanna State Park, Lackawanna County, Pennsylvania, as estimated by grab sampling. Data are pooled across years (2005–2007). The horizontal line within the box represents the median, the box encompasses the interquartile range which contains 50% of the values, and the whiskers encompass the highest and lowest values, excluding outliers. Numbers above the whiskers indicate sample size. According to post-hoc tests there were a number of significant differences in sampled arthropod biomass by vegetation species, with hawthorn and red maple having the highest values (Table 2).

(dogwood, hawthorn, honeysuckle, and *Viburnum*), and controlling for year ($F_{2,823} = 2.7, P = 0.07$) and sample week ($F_{8,823} = 4.0, P < 0.001$), there again was a significant effect of vegetation on invertebrate biomass ($F_{3,823} = 7.0, P < 0.001$). We collected more invertebrates in hawthorn than in all other common shrub species and found that dogwood contained fewer invertebrates than *Viburnum*. Honeysuckle held fewer arthropods than hawthorn and *Viburnum*, but the difference between honeysuckle and dogwood was not significant (Fig. 3).



FIGURE 3. Flightless arthropod abundance by common shrub species in shrub-dominated and forested habitat in or near Lackawanna State Park, Lackawanna County, Pennsylvania, as estimated by grab sampling. Data are pooled across years (2005–2007). The horizontal line within the box represents the median, the box encompasses the interquartile range which contains 50% of values, and the whiskers encompass the highest and lowest values, excluding outliers. Numbers above the whiskers are sample sizes. Different letters indicate statistical significance. More arthropods were found in hawthorn than in any other shrub species.

BIRDS

Survey data. We consistently detected more birds in shrubdominated than in forested habitat in all years (Fig. 4). Shrub habitat contained more species and more individuals than forested habitat and consequently was more diverse (H' forest = 3.9, H' shrub = 4.0; $t_{444} = 2.3$, P < 0.05). After controlling for year (both long-distance and short-distance migrant



FIGURE 4. Bird detections per 100 m of transect by habitat type for long- and short-distance migrants, as estimated by transect surveys. The horizontal line within the box represents the median, the box encompasses the interquartile range which contains 50% of the values, and the whiskers encompass the highest and lowest values, excluding outliers. More migrants were detected in shrub-dominated than in forested habitat in all years.

detections varied significantly among years; long-distance: $F_{2,491} = 129.5$, P < 0.001; short-distance: $F_{2,491} = 10.0$, P < 0.001), the habitat effect was significant for long-distance ($F_{1,491} = 139.2$, P < 0.001) and short-distance ($F_{1,491} = 177.2$, P < 0.001) migrants. There were no significant interactions between terms in either analysis.

Limiting the dataset to those detections prior to 15 May (the early migration period), and controlling for year (long-distance migrant year effect: $F_{2,131} = 13.0$, P < 0.001; short-distance migrant year effect: $F_{2,131} = 0.1$, P = 0.87), the habitat effect remained significant for long-distance ($F_{1,131} = 15.7$, P < 0.001) and short-distance ($F_{1,131} = 67.7$, P < 0.001) migrants: more birds were detected in shrub than in forested habitat. There were no significant interactions between terms in either analysis.

We counted significantly more individuals of several species in shrub than in forested habitat (Table 3). These included not only species that characteristically breed in early successional habitats, but also a number of species that breed in latesuccessional forested habitats. For example, Baltimore Orioles (*Icterus galbula*) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) both had significantly more detections in shrub habitat than in forested habitat. Moreover, the lack of a habitat effect for both the Wood Thrush (*Hylocichla mustelina*) and Veery (*Catharus fuscescens*) implies that individuals were using both forested and shrub-dominated habitats.

Capture data. We captured 4539 individuals of 67 migrant species (Table 4). Our overall bird capture rate (2005, 2006, and 2007 pooled) was 183 birds per 1000 mist-net hours, with forest mist-net captures occurring at a rate of 67 birds captured per 1000 mist-net hours and shrub captures occurring at a rate of 256 birds per 1000 mist-net hours. We captured birds at a higher rate in shrub-dominated habitat than in forested habitat both during the full migration period ($\chi^2_5 = 33.1, P < 0.001$; Table 5) and the early migration period ($\chi^2_5 = 53.8, P < 0.001$). Furthermore, according to our mist-netting data, bird diversity was higher in shrub-dominated habitat (H' forest = 2.9, H' shrub = 3.3; $t_{132} = 2.7, P < 0.01$); we captured more species and more individuals in shrub than in forested habitat.

We captured only one species in forested but not shrubdominated habitat (Yellow-bellied Sapsucker [*Sphyrapicus varius*]), whereas we captured 27 species in shrub-dominated but not forested habitat (Table 4). Moreover, in addition to many early-successional species, many forest-breeding birds used shrub-dominated habitat extensively during stopover, including a number of species that were captured at significantly higher rates in shrub than forested habitat. These included the Wood Thrush, Veery, Red-eyed Vireo (*Vireo olivaceus*), Black-throated Green Warbler (*Dendroica virens*), and Rose-breasted Grosbeak (Table 4).

COMPARING SURVEY AND CAPTURE DATA

We detected 81 migrant landbird species using survey and banding techniques, with 67 species accounted for by our banding data and 70 species by our survey data. Pooling our TABLE 3. Spring detection totals (birds per 100 m of transect) from surveys of landbird migrants in forested and shrub-dominated habitats in or adjacent to Lackawanna State Park, Lackawanna County, Pennsylvania, 2005–2007. Chi-square comparisons were performed on adjusted totals (to correct for differential sampling effort) for species with >24 total detections^a. See Appendix for scientific names of species.

	Detections in	Detections in		
Species	forest per 100 m	shrub per 100 m	χ^2	Р
Alder Flycatcher	0.003	0.090	50.1	< 0.001
Blue-headed Vireo	0.050	0.010	17.4	< 0.001
Red-eyed Vireo	0.390	0.160	58.8	< 0.001
Ruby-crowned Kinglet	0.003	0.060	32.9	< 0.001
Veery	0.140	0.150	0.3	0.61
Hermit Thrush	0.040	0.006	15.8	< 0.001
Wood Thrush	0.120	0.140	1.1	0.29
American Robin	0.020	0.080	23.0	< 0.001
Gray Catbird	0.020	1.030	582.6	< 0.001
Cedar Waxwing	0.030	0.170	61.6	< 0.001
Blue-winged Warbler	0.020	0.420	219.2	< 0.001
Nashville Warbler	0.000	0.100	62.0	< 0.001
Yellow Warbler	0.002	0.370	219.2	< 0.001
Chestnut-sided Warbler	0.007	0.190	102.7	< 0.001
Black-throated Green Warbler	0.270	0.008	151.7	< 0.001
Black-and-white Warbler	0.030	0.210	79.2	< 0.001
American Redstart	0.007	0.060	24.4	< 0.001
Ovenbird	0.610	0.190	138.5	< 0.001
Common Yellowthroat	0.080	0.840	374.4	< 0.001
Scarlet Tanager	0.080	0.020	20.1	< 0.001
Eastern Towhee	0.010	0.360	195.6	< 0.001
Field Sparrow	0.002	0.130	72.8	< 0.001
Song Sparrow	0.070	0.350	109.8	< 0.001
White-throated Sparrow	0.030	0.160	61.0	< 0.001
Rose-breasted Grosbeak	0.010	0.050	14.6	< 0.001
Indigo Bunting	0.020	0.070	15.4	< 0.001
Red-winged Blackbird	0.008	0.040	13.2	< 0.001
Brown-headed Cowbird	0.050	0.090	6.0	0.02
Baltimore Oriole	0.010	0.070	27.2	< 0.001
American Goldfinch	0.030	0.160	61.0	< 0.001
Total	2.980	7.200		

^aThe following species did not meet the criteria of at least 24 detections, but are included in the total. Detected in forest: Yellow-billed Cuckoo, Yellow-bellied Sapsucker, Yellow-throated Vireo, Winter Wren, and Black-throated Blue Warbler. Detected in shrub: American Woodcock, Willow Flycatcher, White-eyed Vireo, Warbling Vireo, House Wren, Blue-gray Gnatcatcher, Brown Thrasher, Tennessee Warbler, Prairie Warbler, Bay-breasted Warbler, Blackpoll Warbler, Mourning Warbler, Wilson's Warbler, Lincoln's Sparrow, and Swamp Sparrow. Detected in both habitats: Black-billed Cuckoo, Northern Flicker, Eastern Wood-Pewee, Eastern Phoebe, Great Crested Flycatcher, Swainson's Thrush, Magnolia Warbler, Yellow-rumped Warbler, Blackburnian Warbler, Northern Waterthrush, Louisiana Waterthrush, Canada Warbler, Chipping Sparrow, Dark-eyed Junco, and Purple Finch.

survey and capture data, we detected 55 species in forest and 76 species in shrub-dominated habitat. Eight landbird species were detected in our surveys but not captured (five in shrub, six in forest, and three in both), and seven species were captured but not detected via surveys (seven in shrub, one in forest, and one in both). Standardized numbers of individuals per species detected using each sampling method were positively correlated (r = 0.6, n = 65, P < 0.001).

DISCUSSION

Our research on spring migration through an inland stopover site suggests that shrub-dominated habitats provide important stopover habitat for landbird migrants. Our results suggest that birds used these habitats in response to both spatial and temporal variation in resource abundance. We captured and counted more species and more individual landbirds in shrubdominated than in forested habitat. We also found shrub habitat to be used extensively by both shrub-nesting species and species known to breed in forested habitat. We trapped more flying invertebrates in shrub-sapling habitats and there was more invertebrate biomass in shrub than in surrounding forests early in the migration period. We also counted and captured more birds in shrub-dominated than forested habitat during this early period.

Few studies have focused on specific structural characteristics of habitats during spring stopover (Rodewald and Brittingham 2007), however those that have have found positive

TABLE 4. Spring capture totals and capture rates (birds per 1000 mist-net hours) of landbird migrants mist-netted in forested and shrubdominated habitats in or adjacent to Lackawanna State Park, Lackawanna County, Pennsylvania, 2005–2007. Chi-square comparisons were performed on adjusted capture totals (to correct for differential sampling effort) for species with >24 total captures^a. See Appendix for scientific names of species.

Species	Forest captures	Forest capture rate	Shrub captures	Shrub capture rate	Total capture rate	χ^2	Р
Red-eyed Vireo	34	3.5	97	6.4	5.5	12.3	< 0.001
Ruby-crowned Kinglet	4	0.4	157	10.3	6.6	139.0	< 0.001
Veery	55	5.7	162	10.6	8.9	22.5	< 0.001
Swainson's Thrush	12	1.2	27	1.8	1.6	1.4	0.24
Hermit Thrush	48	5.0	88	5.8	5.5	0.9	0.35
Wood Thrush	67	7.0	168	11.0	9.5	13.9	< 0.001
American Robin	49	5.1	26	1.7	3.0	25.7	< 0.001
Gray Catbird	47	4.9	708	46.5	32.5	512.9	< 0.001
Brown Thrasher	1	0.1	32	2.1	1.4	27.5	< 0.001
Blue-winged Warbler	8	0.8	146	9.6	6.2	112.0	< 0.001
Nashville Warbler	6	0.6	92	6.0	3.9	67.0	< 0.001
Yellow Warbler	0	0.0	91	6.0	3.7	91.0	< 0.001
Chestnut-sided Warbler	6	0.6	131	8.6	5.5	105.1	< 0.001
Magnolia Warbler	3	0.3	139	9.1	5.7	125.4	< 0.001
Black-throated Blue Warbler	1	0.1	31	2.0	1.3	26.6	< 0.001
Black-throated Green Warbler	5	0.5	25	1.6	1.3	8.9	0.003
Prairie Warbler	0	0.0	40	2.6	1.6	40.0	< 0.001
Black-and-white Warbler	8	0.8	44	2.9	2.2	17.3	< 0.001
American Redstart	1	0.1	55	3.6	2.2	50.4	< 0.001
Ovenbird	174	18.0	221	14.5	16.3	6.0	0.01
Common Yellowthroat	36	3.7	500	32.8	22.9	352.2	< 0.001
Canada Warbler	1	0.1	27	1.8	1.2	22.6	< 0.001
Eastern Towhee	6	0.6	64	4.2	2.8	40.4	< 0.001
Field Sparrow	0	0.0	75	4.9	3.1	75.0	< 0.001
Song Sparrow	2	0.2	53	3.5	2.2	44.2	< 0.001
Lincoln's Sparrow	0	0.0	28	1.8	1.1	28.0	< 0.001
White-throated Sparrow	6	0.6	211	13.8	8.8	184.1	< 0.001
Dark-eyed Junco	1	0.1	27	1.8	1.1	22.6	< 0.001
Rose-breasted Grosbeak	10	1.0	37	2.4	1.9	8.5	0.004
Indigo Bunting	10	1.0	27	1.8	1.5	2.9	0.09
Purple Finch	2	0.2	63	4.1	2.7	54.1	< 0.001
American Goldfinch	0	0.0	44	2.9	1.8	44.0	< 0.001
Total	645	67.1	3894	255.6	182.6		

^aThe following species did not meet the criteria of at least 24 detections, but are included in the total. Captured in forest: Yellow-bellied Sapsucker. Captured in shrub: American Woodcock, Yellow-billed Cuckoo, Black-billed Cuckoo, Yellow-bellied Flycatcher, Acadian Flycatcher, Alder Flycatcher, Willow Flycatcher, Philadelphia Vireo, Carolina Wren, House Wren, Blue-gray Gnatcatcher, Golden-winged Warbler, Tennessee Warbler, Northern Parula, Blackburnian Warbler, Palm Warbler, Bay-breasted Warbler, Mourning Warbler, Wilson's Warbler, Yellow-breasted Chat, Chipping Sparrow, and Fox Sparrow. Captured in both habitats: Northern Flicker, Eastern Phoebe, Blue-headed Vireo, Gray-cheeked Thrush, Cedar Waxwing, Yellow-rumped Warbler, Northern Waterthrush, Scarlet Tanager, Swamp Sparrow, Brown-headed Cowbird, and Baltimore Oriole.

TABLE 5. Comparison of capture rates (captures per 1000 mistnet hours) of short- and long-distance landbird migrants in forested and shrub-dominated habitats during spring migration through two sites in or adjacent to Lackawanna State Park, Lackawanna County, Pennsylvania.

	2005		20	06	2007	
	Shrub	Forest	Shrub	Forest	Shrub	Forest
Short-distance	50.8	10.1	50.7	10.6	60.9 230.3	10.9
Total	250.8	50.8	220.6	40.3 50.9	300.2	90.7

associations between foliage density or structurally complex habitats and number of landbird migrants. For example, foliage density in tree-fall gaps in Illinois was positively associated with songbird abundance (Blake and Hoppes 1986, Martin and Karr 1986). Similar to our findings, Moore et al. (1990) demonstrated that shrub habitat on a Mississippi barrier island held the greatest number of species, had the highest species diversity, and contained the largest number of individuals relative to other habitats present on the island. More recently, Moore and Aborn (2000) documented that Summer Tanagers (*Piranga rubra*) selected shrub habitat over pine forest, marsh, or relic dune habitat on a Mississippi barrier island during spring migration. In addition, Rodewald and Brittingham (2007) demonstrated that both species abundance and species richness of mature forest-breeding migrants was high in edge-dominated forests during spring migration, and these authors suggested that food quality for foliage-gleaning insectivores was relatively high in what they defined as forest-agricultural edge habitat, habitat that was structurally complex. Finally, they proposed that vertical complexity within mature forests may have been attractive to forest-breeding migrants due to a dense, shrubby understory (Rodewald and Brittingham 2007).

For fall migrants, the significance of fruit and fruiting shrubs, which are characteristic of early successional habitats, is well documented (White and Stiles 1992, Parrish 1997, Suthers et al. 2000, McGranahan et al. 2005), including positive dietary effects of consuming a mixed fruit and insect diet (Bairlein and Simons 1995, Bairlein 2003, Podlesak and Mc-Williams 2006). Use of early successional habitats during spring has largely been attributed to higher foliage density and associated invertebrate abundance (Blake and Hoppes 1986, Martin and Karr 1986), and it is likely that we detected more birds in shrub-dominated compared to forested habitat in response to greater resource abundance. Flying arthropod abundance was higher in shrub-dominated habitat in two of three years and more birds were counted and captured in shrub habitat in all three years. This concordance between resource and bird abundance supports the hypothesis that birds were using shrub-dominated habitats in response to resource availability.

An alternative explanation is that migrants were present in shrub habitats in an effort to reduce predation pressure. Shrub-dominated habitat was structurally dense, with more stems and leaves than forested habitat, especially early in the season before leaf-out of canopy trees. Migrant landbirds may use this structure as a way to reduce predation risk, as has been suggested for use of early successional habitats by newly fledged forest-breeding birds (Vitz and Rodewald 2007). Cimprich et al. (2005) demonstrated that Blue-gray Gnatcatchers (Polioptila caerulea) and American Redstarts (Setophaga ruticilla) migrating in fall moved deeper into shrub cover when perceived predation pressure increased. However, over the course of our study we captured or observed very few birdeating raptors. Finally, predators affect foraging behavior, including site choice and foraging rate (Cimprich et al. 2005). Accordingly, the number of predators in an area should influence mass change rates (Dunn 2000). Evidence from our capture data indicates that birds were gaining mass at relatively high rates (RJS et al., unpubl. data), which suggests that individuals were actively foraging and that perceived predation risk was low.

Migrants may use leaf development as a cue in habitat selection (Rodewald and Brittingham 2007) because invertebrate abundance tends to be associated with stage of leaf development. For example, lepidopteran larvae tend to be most numerous in early stages of leaf development, when leaf

quality is higher (Feeny 1970, Futuyma and Gould 1979). As a result, there generally is an association between stage of leafout and abundance of lepidopteran larvae. At our site, birds may have used leaf development as a cue indicating enhanced arthropod abundance in shrub relative to forested habitat. Our shrub habitat sites were dominated by honeysuckle, which completes leaf development prior to native shrubs (Trisel and Gorchov 1994, Gould and Gorchov 2000) and trees (up to two weeks; RJS and MIH, unpubl. data). Consequently, migrants earlier in the season experienced shrub habitats with higher foliage density than nearby forested areas. Although we found no difference in lepidopteran larvae biomass between habitats during the entire migration period, birds appeared to encounter more substrate-dwelling arthropods in shrub habitat than in forested habitat during the early part of migration. Additionally, we documented more invertebrate biomass in shrub-dominated habitat using Malaise traps. Abundant flying invertebrates may have attracted migrant landbirds to shrub habitat.

In our study, migrant detection rates determined using survey and capture methods were significantly correlated. Similarly, Carlisle et al. (2004) and Wang and Finch (2002) found general agreement between their survey and capture data. While we detected a few species with one technique and not the other, using both methods to assess habitat use reduces inherent biases present in either method and more accurately portrays the migrant community (Rappole et al. 1998, Wang and Finch 2002, Swanson et al. 2003). Moreover, results from each sampling technique are in general agreement-shrubdominated habitat held more species and more individuals than forested habitat, and this effect was evident across all three years of our study. Constancy in relative abundances at our sites across years suggests that choice of habitat was based on a characteristic associated with that habitat (Martin and Karr 1986), and implies that shrub-dominated habitats were of higher quality than forested habitats at our site in northeastern Pennsylvania. Finally, general concordance of results from these two disparate sampling methods enhances the validity of our interpretation that shrub habitats in northeastern Pennsylvania provide quality stopover habitat for migrating landbirds.

CONSERVATION IMPLICATIONS

Transitional, early successional habitats in eastern North America are becoming scarce (Askins 2000, Oehler 2003, Rich et al. 2004). To date, most of the concern about losing these habitats has centered on reduction of breeding habitat for shrub-nesting species; indeed, a number of shrub-nesting species are declining (Askins 2001, Rich et al. 2004) and these declines have been at least partly attributed to loss of quality breeding habitat (Hunter et al. 2001). However, increasing evidence points to the importance of early successional habitats during the postfledgling to premigratory period (Vitz and Rodewald 2007; RJS and MIH, unpubl. data), as well as during spring and fall migration, both for species that characteristically breed in these habitats and species that breed in late-successional habitats. While further study is necessary to elucidate the mechanisms behind these habitat choices, it is becoming increasingly clear that shrub habitats are important to migrating and breeding landbirds and warrant conservation efforts.

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APPENDIX.	Common and scientific n	ames and migratory cate	gory of landbirds ca	ptured or counted duri	ng spring migration,	, 2005–2007,
Lackawanna (County, Pennsylvania.					

Migratory category	Species	Migratory category	Species
Short-distance	Yellow-bellied Sapsucker (Sphyrapicus varius) Northern Flicker (Colaptes auratus) Eastern Wood-Pewee (Contopus virens) ^a Eastern Phoebe (Sayornis phoebe) Great Crested Flycatcher (Myiarchus crinitus) ^a Carolina Wren (Thryothorus ludovicianus) ^a Winter Wren (Troglodytes troglodytes) ^a Ruby-crowned Kinglet (Regulus calendula) Hermit Thrush (Catharus guttatus) American Robin (Turdus migratorius) Brown Thrasher (Toxostoma rufum) Cedar Waxwing (Bombycilla cedrorum) Yellow-rumped Warbler (Dendroica coronata) Palm Warbler (Dendroica palmarum) ^b Eastern Towhee (Pipilo erythrophthalmus) Chipping Sparrow (Spizella passerina) Field Sparrow (Spizella pusilla) Fox Sparrow (Melospiza melodia) Lincoln's Sparrow (Melospiza lincolnii) Swamp Sparrow (Melospiza georgiana) White-throated Sparrow (Zonotrichia albicollis) Dark-eyed Junco (Junco hyemalis) Red-winged Blackbird (Agelaius phoeniceus) Brown-headed Cowbird (Molothrus ater) Purple Finch (Carduelis tristis)	Long-uistance	Veery (<i>Catharus fuscescens</i>) Gray-cheeked Thrush (<i>Catharus minimus</i>) ^b Swainson's Thrush (<i>Catharus ustulatus</i>) Wood Thrush (<i>Hylocichla mustelina</i>) Gray Catbird (<i>Dumetella carolinensis</i>) Blue-winged Warbler (<i>Vermivora pinus</i>) Golden-winged Warbler (<i>Vermivora chrysoptera</i>) ^b Tennessee Warbler (<i>Vermivora peregrine</i>) Nashville Warbler (<i>Vermivora peregrine</i>) Nashville Warbler (<i>Vermivora ruficapilla</i>) Northern Parula (<i>Parula americana</i>) ^b Yellow Warbler (<i>Dendroica petechia</i>) Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>) Magnolia Warbler (<i>Dendroica magnolia</i>) Black-throated Blue Warbler (<i>Dendroica caerulescens</i>) Black-throated Green Warbler (<i>Dendroica virens</i>) Blackburnian Warbler (<i>Dendroica fusca</i>) Prairie Warbler (<i>Dendroica striata</i>) ^a Blackpoll Warbler (<i>Dendroica striata</i>) ^a Black-and-white Warbler (<i>Mniotilta varia</i>) American Redstart (<i>Setophaga ruticilla</i>) Ovenbird (<i>Seiurus aurocapilla</i>) Northern Waterthrush (<i>Seiurus noveboracensis</i>) Louisiana Waterthrush (<i>Seiurus motacilla</i>) ^a Mourning Warbler (<i>Oporornis philadelphia</i>) Common Yellowthroat (<i>Geothlypis trichas</i>) Wilson's Warbler (<i>Wilsonia pusilla</i>)
Long-distance	 Yellow-billed Cuckoo (Coccyzus americanus) Black-billed Cuckoo (Coccyzus erythropthalmus) Ruby-throated Hummingbird (Archilochus colubris) Yellow-bellied Flycatcher (Empidonax flaviventris)^b Acadian Flycatcher (Empidonax virescens)^b Alder Flycatcher (Empidonax alnorum) Willow Flycatcher (Empidonax traillii) White-eyed Vireo (Vireo griseus)^a Yellow-throated Vireo (Vireo flavifrons)^a Blue-headed Vireo (Vireo solitaries) Warbling Vireo (Vireo gilvus)^a Philadelphia Vireo (Vireo niladelphicus)^b Red-eyed Vireo (Vireo olivaceus) House Wren (Troglodytes aedon) 		Yellow-breasted Chat (<i>Icteria virens</i>) ^b Scarlet Tanager (<i>Piranga olivacea</i>) Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>) Indigo Bunting (<i>Passerina cyanea</i>) Baltimore Oriole (<i>Icterus galbula</i>)

^aDetected by 50 m fixed-width line transects, but not captured in mist nets. ^bCaptured in mist nets, but not detected by 50 m fixed-width line transects.