The Wilson Journal of Ornithology 122(4):725–737, 2010

MIGRANT SONGBIRD SPECIES DISTRIBUTION AND HABITAT USE DURING STOPOVER ON TWO ISLANDS IN THE GULF OF MAINE

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ABSTRACT.—We compared the distribution of migrant bird species between two islands in the Gulf of Maine to examine if differences in habitat resulted in differences in avian species composition and relative abundance during stopover. Ninety-one species were captured on both islands and those species captured on only one island were either breeding species or rare visitors to the islands. Differences in bird species distribution between islands were species-specific and consistent among sampling periods for nearly all species. Twelve species were captured more frequently on Star Island and 11 species more frequently on Appledore Island. Stopover species distribution appeared to be related to habitat structure, vegetation, diet, and habitat area. Scrub-shrub/open habitat breeding species and forest breeding species were not evenly distributed between islands. Island use was most closely associated with breeding habitat. All but two of the eight species that breed in scrub-shrub or open habitat were captured more frequently on Star Island. Ten of the species more common on Appledore Island breed in forested habitat. Nine of the 11 species more common on Appledore Island are area-sensitive in breeding areas, suggesting potential area sensitivity during migration. Differential habitat use indicates a large number of stopover sites in a wide variety of habitats are necessary to meet migration needs of passerine species. *Received 17 November 2006. Accepted 22 April 2010.*

Suitable stopover habitat is critical to a successful migration (Moore et al. 1995) and loss of stopover habitat may be a factor in long-term population declines (Sherry and Holmes 1995, Finch and Wang 2000, Hutto 2000). Migrants have increased risk of mortality during migration (Bairlein 1992; Moore et al. 1992, 1995; Hutto 1998; Sillett and Holmes 2002.) without habitat that can satisfy their needs to replenish critical energy supplies, reorient (Baird and Nisbet 1960), escape adverse winds and weather, recover from muscle fatigue or injury, and avoid the dehydration of daytime flight. More information is needed on habitat requirements of passerines during migration (Moore et al. 1992, 1995; Sherry and Holmes 1995; Hutto 2000; Petit 2000) to understand what constitutes valuable stopover habitat and influences habitat selection (Moore et al. 1995, Dunn 2000).

Migrants show differential habitat use including species-specific distribution among stopover habitats (Hutto 1985, Moore et al. 1990, Winker 1995), but the basis for habitat selection is not clear. Finch and Wang (2000) reported bird densities during migration were affected by vegetation structure and habitat type, but few studies have examined fine-scale habitat relationships during migration (Rodewald and Brittingham 2004). There is some evidence that songbirds may select stopover habitat with vegetative characteristics similar to their breeding habitat (Parnell 1969, Petit 2000). Other factors affecting stopover habitat use may include suitability to a species' foraging method (Bairlein 1992), food availability (Hutto 1985, Moore et al. 1995), dietary shifts (Parrish 2000), predation and competition (Moore et al. 1992), and site characteristics including area (Moore et al. 1995), temperature, and humidity (Winker 1995).

Star and Appledore islands are part of the Isles of Shoals on the New England coast, USA. They provide a unique opportunity to examine the relationship between habitat and migrant stopover patterns because large numbers of songbirds stop at the archipelago during spring and fall migrations (Morris et al. 1994, 1996), and the islands are <1 km apart. Weather and body mass can influence selection of stopover sites (Moore and Simons 1992) and the potential confounding effect that different weather conditions have on migration behavior can be eliminated by comparing two adjacent sites. Both islands are categorized as maritime shrub thicket (Sperduto and Nichols 2004), which encompasses a range from low-growing shrubs to tall thickets; comparison of these islands presents an opportunity to examine the relationship of birds and stopover habitat at a fine scale. Species richness and abundance in

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migration may be correlated with patch size (Martin 1980, Blake 1986, Somershoe and Chandler 2004), as has been shown during the breeding season when number of species and individuals increases with area (Freemark and Merriam 1986, Blake and Karr 1987, Faaborg et al. 1995). Star Island is smaller than Appledore Island allowing consideration of area effects on species composition during stopovers.

Our objectives were to examine: (1) whether there were differences in species richness, composition, and distribution between the islands; and (2) whether a species' breeding habitat or food habits were related to stopover habitat use. We predicted more species would be captured on Appledore Island and that habitat differences between islands would result in differences in species composition and frequency of capture.

METHODS

Study Site.—The Isles of Shoals is a group of nine small islands and several ledges in the Gulf of Maine, 14.5 km southeast of Portsmouth, New Hampshire (42° 58′ N, 70° 36′ W), and 9.7 km from the nearest point of the mainland. Appledore Island, Maine is the largest of the islands at 33.6 ha and Star Island, New Hampshire is 13.4 ha. The minimum shore-to-shore distance between Star and Appledore islands is ~0.7 km and the study sites were 1.6 km apart.

Bird Surveys.—Bird surveys were conducted simultaneously on both islands in 1999 and 2000 using mist nets during spring and fall migration following the protocol established for the Appledore Island Migration Banding Station (Morris et al. 1994, 1996). There were four sampling periods: 11 May–8 June 1999, 10 May–8 June 2000, and 16 August–30 September 1999 and 2000. Weather permitting, mist nets (6 or 12 × 2.6 m, 4 shelves, 30 mm mesh) were operated during daylight hours with the nets opened just before sunrise, closed at sunset, and checked every 30 min throughout the day. Up to five nets were operated on Star Island and up to 10 nets were operated on Appledore Island. Captured birds were brought to a central location on each island and banded with USGS aluminum bands.

Habitat Surveys.—We collected habitat data at net sites rather than at random locations distributed over each entire island. There is extreme landscape variability on both islands with habitat ranging from rocky splash zones or mowed lawns to thick scrub-shrub relatively close to the nets. We characterized the natural vegetation that surrounded the mist nets to ensure data were representative of the habitat used by the species captured. These data should not be considered representative of the habitat on the entire island.

Vegetative structure and composition at each site were measured using a modified version of James and Shugart (1970) and Winker et al. (1992). We established eight circular survey plots, each centered on a pair of mist nets (or a single net, if there was only one in a given area). There were three plots on Star Island and five on Appledore Island covering all net locations. Each plot was 0.04 ha (radius = 11.35 m) and was divided into two semicircles, separated by the net lane (1–2 m) to remove the non-vegetated lane from analysis.

We established six 1.5 m-diameter circular subplots in each plot using a stratified random design so each subplot was entirely within the larger plot. Subplots were located by extending a random distance into alternating halves of the plot from six equidistant points (3.94 m apart) along the diameter of the plot, excluding the outer 1.5 m. We established a 1 m-wide transect in each half of the plot to measure shrub density. Transects were parallel to the net lane and 0.3 m from the edge of the net lane to reduce the influence of trimming along net lanes.

We defined trees as woody stems with a diameter at breast height (dbh) ≥3.0 cm and shrubs as any woody vegetation <3.0 cm dbh and over 0.75 m in height. We recorded live tree species, height, and dbh (0.1-cm diameter tape) in each plot. We recorded only dbh for dead trees. We recorded species and height for each live shrub stem in the transect, and counted stems separately if they branched within 0.1–0.2 m above the ground. We counted the number of stems for dead shrubs. Heights for live trees and shrubs were measured to the nearest 0.1 m. Separate measurements were taken for each species in a cluster.

We measured herbaceous cover, canopy cover, and vegetation density in each subplot. We visually estimated herbaceous cover in each subplot to the nearest 5%. We visually estimated canopy cover from the center of each subplot and recorded cover to the nearest 5% at six 1-m height classes beginning with 0–1.0 m (to account for low woody plant cover that functions as canopy for ground-feeding birds). We used a density board (Nudds 1977) placed at the center of a

subplot to measure vegetation density and estimated percent cover from 2 m distant, rather than the recommended 15 m (Nudds 1977), because of the extreme density of the shrub vegetation. We chose a random direction using eight possible points of the compass and rejected points that were outside the full plot after walking 2 m from the board. We recorded vegetation cover to the nearest 5% in each of the four sections of the density board (0–0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0 m).

All habitat data were collected between 6 May and 10 June 2000 by RWS to eliminate variability among observers. Subplot measurements were obtained between 5 and 10 June to ensure that vegetation density and canopy cover measurements were at the same time after leaf out.

Data Analysis.—We used Systat Version 10 (SPSS Inc. 2000) for statistical analyses. The analyses, except bird species richness, include only those species that do not breed on the Isles of Shoals (i.e., only stopover migrants). We used raw counts of birds captured for all Chi-square tests.

We used a heterogeneity Chi-square analysis (Zar 1999) to test for differences in species distribution between islands and analyzed each sampling period separately. We used Freeman-Tukey deviates in Systat to examine which species were responsible for significant Chi-square tests. We removed those species from the analysis until there was no difference ($P > 0.05$) between islands. Expected values for individual species were calculated using the total number of migrant birds captured on each island. The heterogeneity test was the prime analysis used in examining differences between islands, even though expected values for some species were below the desired criteria for Chi-square tests. We used a Chi-square goodness-of-fit test for each species as a secondary analysis to compare number of individuals captured between islands without violating the expected value criteria. Expected values were ≥ 5 in all tests except Purple Finch (*Carpodacus purpureus*) and Savannah Sparrow (*Passerculus sandwichensis*) in spring 2000.

We followed Jones et al. (2002) and the recommendations of Gotelli and Ellison (2004), and did not use Bonferroni corrections in the analyses to reduce the likelihood that real differences or relevant patterns would be missed. Bonferroni corrections are not as practical for diverse communities requiring multiple statistical tests (Moran 2003) such as the number of migrant birds in this study. It is unlikely the results from all tests will be spurious (Moran 2003).

Species were included in the distribution analysis if there were ≥ 10 individuals banded on at least one island in any two sampling periods, and were analyzed in only those sampling periods when their numbers met this minimum criterion. The only exception was Purple Finch, which is an irruptive migrant present in large numbers during fall 1999 only. We included it in the spring 2000 analysis, although only eight individuals were banded, to examine if the return migration in spring had the same distributional pattern. Recaptures were not included in the distribution analysis.

We used a Mann-Whitney *U*-test to compare mean number of tree and shrub stems per plot between islands for each species with more than 20 stems on one of the islands. We computed the mean per plot for each island and compared means between islands using a Mann-Whitney *U*-test for the habitat data: live tree and shrub density (all species combined), dead tree and shrub density, tree and shrub height, and tree dbh. A mean for each individual plot was calculated first for the latter three measures, which were used to calculate the mean per plot for the entire island. We divided tree heights into five 1-m height classes beginning with 2.0 m and shrub heights into five 0.5-m height classes beginning with 0.5 m. We compared the distribution of trees and shrubs by height class between islands with a heterogeneity Chi-square analysis, and used a Mann-Whitney *U*-test to examine differences among mean number of stems per plot in each height class. We divided tree dbh into seven size classes: 3–3.9, 4–4.9, 5–5.9, 6–6.9, 7–10.9, 11–15.9, and ≥ 16.0 cm. The larger size classes with few trees were combined to create suitably sized groupings. We compared the distribution of trees by dbh class between islands with a heterogeneity Chi-square analysis. We used ANOVA to compare percent herbaceous cover between islands and MANOVA with associated univariate tests, when the MANOVA was significant, to compare mean vegetation density at four height classes and canopy cover at six height classes between islands.

We assigned habitat types to each bird species for breeding habitat to compare species differences between islands with habitat associations in breeding areas. Habitat classifications were: early successional, forest, forest edge, low forests at high elevations and in bogs, scrub-shrub, and open areas (including grasslands and emergent wet-

lands). We also examined vegetation type and area sensitivity in breeding areas. Area sensitivity information was obtained from Robbins et al. (1989) and Birds of North America species accounts (Poole and Gill 1993–1997, 1998–2002); breeding habitat information was primarily from DeGraaf and Yamasaki (2001) supplemented by Ehrlich et al. (1988). We classified fall frugivory into four categories using the mean percent of fruit in fecal samples during fall migration on Block Island, Rhode Island (Parrish 1997): low 0–29, medium 30–59, medium-high 60–89, and high 90–100%.

RESULTS

Bird Species Richness.—We banded 5,443 birds (3,833 migrants) on Star Island and 8,372 (6,604 migrants) on Appledore Island during the four sampling periods. Mean (± SD) captures for Star Island were 1,234 ± 28.3 in spring and 1,487 ± 255.3 in fall, and for Appledore Island were 2,140 ± 302.6 in spring and 2,046 ± 233.3 in fall. Ninety-nine species were captured on Star Island and 102 on Appledore Island; 91 of the species were captured on both islands. Mean (± SD) species richness for all sampling periods combined was 68 ± 4.65 for Star Island and 74 ± 3.16 for Appledore Island. Mean (± SD) species richness during spring was 64 ± 0.71 on Star Island and 71 ± 0.71 on Appledore Island; during fall it was 72 ± 0.71 on Star Island and 76 ± 2.12 on Appledore Island.

Eight species were captured only on Star Island and 11 species only on Appledore Island. Some species were captured infrequently and were rare visitors to the Isles of Shoals or unusual captures in songbird mist nets. More of these "accidental" species would be expected on Appledore Island due to probability (more net hours). Species richness on the two islands was identical at 70 species with 100% overlap in species composition between the islands when we removed breeding and accidental species from the analysis.

Bird Species Distribution.—The distribution of migrant species between islands differed in each sampling period (spring 1999: $\chi^2 = 242.27$, df = 28, $P \leq 0.001$; spring 2000: $\chi^2 = 206.19$, df = 33, $P \leq 0.001$; fall 1999: $\chi^2 = 325.92$, df = 31, $P \leq 0.001$; fall 2000: $\chi^2 = 400.69$, df = 34, $P \leq 0.001$). The difference between islands was attributed to a fairly consistent group of species (Table 1). Twelve species were captured more frequently than expected on Star Island (scientific names in Table 1): Traill's Flycatcher, Ruby-crowned Kinglet, Cedar Waxwing, Magnolia Warbler, Yellow-rumped Warbler, Wilson's Warbler, Yellow-breasted Chat (fall, not tested in spring), Savannah Sparrow (spring, not tested in fall), Lincoln's Sparrow (fall but not spring), Swamp Sparrow, White-throated Sparrow (fall but not spring), and Purple Finch. Eleven species were captured more frequently than expected on Appledore Island (Table 1): Red-eyed Vireo, Brown Creeper (fall, not tested in spring), Veery (fall but not spring), Swainson's Thrush (spring but not fall), Black-throated Blue Warbler, Black-and-white Warbler, American Redstart (fall but not spring), Ovenbird, Northern Waterthrush, Mourning Warbler (spring but not fall), and Canada Warbler (spring but not fall).

Habitat.—Thirteen species of shrubs and eight species of trees were recorded on Star Island and 15 species of shrubs and nine species of trees on Appledore Island (Table 2). The most common shrub species in the netting area on Star Island were chokeberry, raspberry, and rose; the most common trees were winterberry, sumac, and bayberry (scientific names in Table 2). The most common shrubs in the netting area on Appledore Island were chokecherry, winterberry, and arrowwood; the most common trees were chokecherry, serviceberry, and arrowwood. Only raspberry and winterberry were in the top five species on both islands; the other dominant species were typically scarce or absent on the other island. Bayberry and huckleberry were recorded only on Star Island, and apple, arrowwood, black cherry, and pin cherry were recorded only on Appledore Island.

The mean number of trees on Appledore Island was higher than on Star Island, but this difference was not significant for all heights combined (Table 3). One Star Island plot had 228 trees, but the mean of the two remaining plots was only 65 trees. No plot on Appledore Island had <142 trees. The distribution of trees over five height classes differed ($\chi^2 = 375.5$, df = 4, $P \leq 0.001$) between islands (Fig. 1). Appledore Island had more trees per plot in the highest three classes and Star Island had more in the lowest class. The difference between islands was not significant for the 3–3.9 m height class. There were also fewer dead trees per plot on Star Island than Appledore Island (Table 3).

Trees on Star Island had a smaller mean dbh per plot (range = 3.0–10.7 cm) than Appledore Island (range = 3.0–33.2 cm; Table 3). The distribution

of trees over seven dbh classes differed (χ^2 = 50.6, df = 6, $P \leq 0.001$) between islands with fewer trees on Star Island in all dbh classes, and fewer than 10 trees in the four classes greater than 6.0 cm. Star Island had shorter mean tree height per plot than Appledore Island (Table 3). There were only six trees taller than 4.0 m on Star Island (3 plots), whereas Appledore Island had 529 that were 4.0 m or taller (5 plots).

Shrub density was higher on Star Island than Appledore Island, primarily because of a difference in the number of small-diameter shrubs (Table 3). Star Island had more dead shrubs per plot than Appledore Island but the difference was not significant (Table 3). Overall mean shrub height did not differ between islands (Table 3). However, distribution of shrubs over five height classes (Fig. 1) differed (χ^2 = 729.5, df = 4, $P \leq 0.001$) between islands. Star Island had significantly more shrubs per plot in the lowest three classes and Appledore had significantly more in the highest height class. There was no difference (P = 0.881) between islands in the 2–2.4 m class.

There was a slight difference between islands in vegetation density for all four heights combined ($F_{4,43}$ = 2.48, P = 0.058). Star Island had significantly higher mean percent cover than Appledore Island in the lowest two height classes (0–0.5 and 0.5–1.0 m) but there was no significant difference in the two upper heights.

Percent canopy cover differed ($F_{6,41}$ = 4.25, P = 0.002) between islands. Star Island had higher percent cover in the lowest two height classes from 0.0 to 2.0 m, and Appledore Island had higher percent cover in the highest three classes (3.1 m and higher); one height class (2.1–3.0 m) did not differ between islands. Star Island had mean (± SD) herbaceous cover of 52.5 ± 34.2% and Appledore Island had a mean cover of 35.8 ± 35.0%, but the difference was not significant ($F_{1,46}$ = 2.69, P = 0.112).

Comparison of Bird Distribution with Habitat.—There were fewer trees on Star Island and they were smaller in height and dbh than Appledore Island which had only six trees taller than 4.0 m (3 plots), whereas Appledore Island had 529 that were 4.0 m or taller (5 plots). Star Island had more shrubs in all height classes except the tallest (>2.5 m), and had the highest vegetation density in all height classes except the highest (1.5–2.0 m). Appledore Island had more canopy cover except in the 0–2.0 m range. Thus, Star Island more closely resembled a typical scrub-shrub habitat in structure while taller thickets with higher canopy cover characterized Appledore Island. This difference allowed us to compare differences in bird distribution between islands in relation to habitat (Table 4).

There were significant differences in distribution between islands (χ^2 = 4.5, df = 1, P = 0.033) when bird species were grouped based on breeding habitat as (1) scrub-shrub or open, or (2) forest. Six of the eight species that breed in scrub-shrub or open habitat were captured significantly more frequently on Star Island (Table 4); one of the other two showed no difference between islands (Chestnut-sided Warbler) and the other was more numerous on Appledore Island (Mourning Warbler). Six of 32 forest-breeding species were more common on Star Island, 10 were more common on Appledore Island, and 16 showed no difference between islands (Table 4). Nine of 12 forest-breeding species that are area-sensitive in breeding areas were more common on Appledore Island, and the other three species showed no difference between islands (Table 4).

DISCUSSION

Star Island more closely resembled a typical scrub-shrub habitat in structure with denser shrub vegetation, more trees, and greater canopy cover <3.0 m. Appledore Island had greater tree density, canopy cover, and shrub density >3.0 m. Bird species richness and composition varied minimally between islands; however, relative abundance of some species varied greatly probably because of vegetation differences. These results are consistent with Rodewald and Brittingham (2004) who reported relative abundance during migration varied among habitats despite broad habitat use by all species.

Differences in species distribution between Star and Appledore islands were species-specific and consistent between sampling periods. Bairlein (1983) and Moore et al. (1990) also reported high consistency of species-specific habitat distributions and that migrants show selective use of certain habitats. There was no consistent relationship to winter habitat but there was to breeding habitat.

Most migrant species that breed in scrub-shrub and open habitat were more numerous on Star Island, except for Chestnut-sided and Mourning warblers. The shorter vegetation on Star Island

TABLE 1. Bird species distribution between Star Island (SI) and Appledore Island (AP) based on banding data from 1999 and 2000. H/g = Chi-square heterogeneity and goodness-of-fit analyses; H = species responsible for the difference between islands. A — indicates no difference between the islands and blank = capture numbers insufficient for analysis in that sampling period. Island = location where relatively more of that species were captured.

		Spring							Fall						
		1999			2000				1999			2000			
Species	Scientific name	SI	AP	H/g	SI	AP	H/g	Island	SI	AP	H/g	SI	AP	H/g	Island
Northern Flicker	*Colaptes auratus*	1	2		0	2			19	43	−/−	8	17	−/−	—
Eastern Wood-Pewee	*Contopus virens*	14	38	−/−	25	38	−/−	—	5	6		11	20	−/−	—
Yellow-bellied Flycatcher	*Empidonax flaviventris*	8	27	−/−	29	48	−/−	—	6	20	−/g+	19	44	−/g+	—
Traill's Flycatcher	*E. traillii/alnorum*	32	25	H/g**	50	50	H/g**	SI	18	15	H/g+	34	34	—	SI
Least Flycatcher	*E. minimus*	5	9		24	40	−/−	—	6	25	−/g*	35	22	H/g**	Both
Eastern Phoebe	*Sayornis phoebe*	0	1		0	0			12	20	−/−	5	11	−/−	—
Blue-headed Vireo	*Vireo solitarius*	6	23	−/−	6	28	−/g*	AP	9	21	−/−	19	10	H/g**	SI
Philadelphia Vireo	*V. philadelphicus*	0	0		1	6			6	14	−/−	17	32	−/−	—
Red-eyed Vireo	*V. olivaceus*	26	156	H/g**	62	164	H/g**	AP	69	230	H/g**	116	354	H/g**	AP
Red-breasted Nuthatch	*Sitta canadensis*	5	7		4	10	−/−	—	32	94	−/ g**	0	2		—
Brown Creeper	*Certhia americana*	1	0		0	0			5	33	H/g**	4	16	H/g+	AP
Golden-crowned Kinglet	*Regulus satrapa*	0	0		1	1			14	26	−/−	71	94	−/−	—
Ruby-crowned Kinglet	*R. calendula*	47	28	H/g**	16	5	H/ g**	SI	9	21	−/−	40	37	−/g*	(SI)
Veery	*Catharus fuscescens*	4	12	−/−	5	10	−/−	—	2	10	−/−	4	17	H/g*	AP
Swainson's Thrush	*C. ustulatus*	2	33	H/ g**	13	40	−/g+	AP	6	14	−/−	5	15	−/−	—
Cedar Waxwing	*Bombycilla cedrorum*	10	7	H/g**	26	14	H/g**	SI	56	70	H/−	76	50	H/g**	SI
Nashville Warbler	*Vermivora ruficapilla*	7	12	−/−	11	18	−/−	—	10	9	−/−	32	52	−/−	—
Northern Parula	*Parula americana*	24	103	−/g*	14	33	−/−	—	11	12	−/−	13	8	−/g*	—
Chestnut-sided Warbler	*Dendroica pensylvanica*	16	33	−/−	17	17	−/g*	—	1	9		8	16	−/−	—
Magnolia Warbler	*D. magnolia*	137	258	H/g*	159	254	−/−	SI	23	24	H/−	57	61	−/g+	SI
Black-throated Blue Warbler	*D. caerulescens*	16	74	−/g*	7	25	−/g+	AP	15	53	−/g**	11	53	H/g**	AP
Yellow-rumped Warbler	*D. coronata*	20	14	H/g**	30	12	H/g**	SI	199	47	H/g**	145	20	H/g**	SI
Black-throated Green Warbler	*D. virens*	11	19	−/−	13	12	−/−	—	7	8		12	17	−/−	—
Blackburnian Warbler	*D. fusca*	5	13	−/−	16	16	−/−	—	2	1		3	3		
Blackpoll Warbler	*D. striata*	27	106	−/g+	51	88	−/−	—	45	75	—	29	27	−/g+	—
Black-and-white Warbler	*Mniotilta varia*	18	72	−/g+	10	56	H/g**	AP	14	45	−/g*	33	93	H/g**	AP
American Redstart	*Setophaga ruticilla*	42	138	−/−	67	133	−/−	—	34	96	−/g**	85	208	H/g**	AP
Ovenbird	*Seiurus aurocapilla*	7	112	H/g**	10	59	H/g**	AP	2	21	H/g**	7	35	H/g**	AP
Northern Waterthrush	*S. noveboracensis*	10	57	−/g*	8	39	H/g**	AP	66	133	−/g+	100	228	H/g**	AP
Mourning Warbler	*Oporornis philadephia*	9	17	−/−	6	29	H/g*	AP	10	10	−/−	13	18	−/−	—
Wilson's Warbler	*Wilsonia pusilla*	12	11	H/g*	38	18	H/g**	SI	18	20	H/−	53	37	H/g**	SI
Canada Warbler	*W. canadensis*	12	34	−/−	9	60	H/g**	AP	1	5		13	31	−/−	—

TABLE 1. Continued.

Species	Scientific name	Spring							Fall						
		1999			2000				1999			2000			
		SI	AP	H/g	SI	AP	H/g	Island	SI	AP	H/g	SI	AP	H/g	Island
Yellow-breasted Chat	*Icteria virens*	0	0		0	1			31	24	H/g*	28	7	H/g**	SI
Savannah Sparrow	*Passerculus sandwichensis*	13	6	H/g**	10	1	H/g**	SI	2	0		0	0		
Lincoln's Sparrow	*Melospiza lincolnii*	2	9		21	28	−/−	—	11	2	H/g**	10	3	H/g**	SI
Swamp Sparrow	*M. georgiana*	45	31	H/g**	26	17	H/g**	SI	7	2		17	4	H/g**	SI
White-throated Sparrow	*Zonotrichia albicollis*	39	70	−/−	29	63	−/−	—	95	119	H/−	28	26	−/g+	SI
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	3	16	−/−	9	25	−/−	—	6	2		6	3		
Baltimore Oriole	*Icterus galbula*	4	9		8	12	−/−	—	17	25	−/−	19	30	−/−	—
Purple Finch	*Carpodacus purpureus*	0	0		8	2	H/g**	SI	42	31	H/g**	0	0		SI

+ = $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and − = differences not significant.

with its greater density at lower heights and scarcity of taller trees may be more suitable for scrub-shrub species than Appledore Island. Bairlein (1983) also reported differences in species along a gradient of vegetation density, and Rodewald and Brittingham (2004) reported shrub-sapling breeding species were most abundant in early successional and edge habitat during fall stopover.

Ten of the 11 migrant species captured significantly more frequently on Appledore Island breed in forested habitat with the exception being Mourning Warbler. However, not all forest-breeding species were more numerous on Appledore Island. Nine of the 10 forest-breeding species that were more numerous on Appledore Island are area-sensitive in breeding areas. No area-sensitive species was more numerous on Star Island. Other studies have reported evidence of area-sensitivity during migration (Martin 1980, Cox 1988, Somershoe and Chandler 2004). The influence of patch size on stopover habitat use is also influenced by microhabitat and landscape (Petit 2000). The influence of habitat area in our study was not reliably separated from habitat structure. For example, area-sensitive species may be less flexible in migration stopover habitat than other forest breeding species and, thus, more common on Appledore Island because of its more forest-like habitat.

Microhabitat factors likely contributed to the distribution patterns of forest-breeding species. American Redstart breed in habitat with a dense sapling (2.5–9.9 cm dbh) understory (DeGraaf and Yamasaki 2001). Appledore Island had far more trees in this size class than Star Island. Appledore Island also had more and larger trees than Star Island. Black-and-white Warblers were recorded only on large limbs of larger trees during spring migration in Kentucky (Mason 1979) and were more common on Appledore Island. Brown Creeper was the only forest-breeding species more common on Appledore Island that is not area-sensitive. It forages primarily on large-diameter trees with deeply furrowed bark (Hejl et al. 2002). This feeding substrate is almost totally lacking on Star Island but is present on Appledore Island.

Fruit availability also seemed to affect the distribution of species. Three of the six species more numerous on Star Island that were not scrub-shrub or open habitat breeders appeared to be influenced by presence of fruit-bearing shrubs.

TABLE 2. Tree and shrub species composition on Star and Appledore islands sampling plots (0.04 ha) in 2000. Differences in means based on Mann-Whitney *U*-tests for between islands. A — indicates insufficient numbers for analysis (20 or fewer stems). Species with <10 stems (total trees and shrubs combined) on both islands were not analyzed[c].

		Star Island		Appledore Island		Difference	
		Shrubs	Trees	Shrubs	Trees		
Common name	Scientific name	Mean per plot	Mean per plot	Mean per plot	Mean per plot	shrubs	trees
Apple	*Pyrus malus*	—	—	0.6	4.0		
Arrowwood	*Viburnum recognitum*	—	—	56.0	23.6	+	+
Northern bayberry	*Myrica pensylvanica*	35.3	12.0	—	—	+	+
Blackberry	*Rubus allegheniensis*	12.3	—	9.4	—	−	
Black cherry	*Prunus serotina*	—	—	—	10.0		*
Chokeberry[a]	*Pyrus* spp.[a]	430.7	—	0.8	—	*	
Chokecherry	*Prunus virginiana*	3.3	9.0	87.8	55.0	*	*
Huckleberry	*Gaylussacia baccata*	11.3	—	—	—	−	
Pin cherry	*Pyrus pensylvanica*	—	—	2.8	11.8		−
Poison ivy	*Toxicodendron radicans*	19.0	1.0	—	0.4	+	
Raspberry	*Rubus ideaus*	296.0	—	30.2	—	−	
Rose[b]	*Rosa* spp.[b]	158.0	—	13.4	—	*	
Serviceberry	*Amelanchier* spp.	1.0	6.7	2.0	46.6		*
Staghorn sumac	*Rhus typhina*	1.0	19.3	5.4	9.6	−	−
Winterberry	*Ilex verticillata*	76.3	68.3	57.2	36.2	−	−

+ = $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and − = differences not significant.

[a] Red and purple chokeberry (*P. arbutifolia, P. floribunda*) and possible hybrids.

[b] Virginia rose (*R. virginiana*) on both islands, pasture rose (*R. carolina*) only on Appledore Island.

[c] Species with fewer than 10 stems: carrion-flower (*Smilax herbacea*), common elder (*Sambucus canadensis*), bittersweet nightshade (*Solanum dulcamara*), red cedar (*Juniperus virginiana*), red maple (*Acer rubrum*), Virginia creeper (*Parthenocissus quinquefolia*).

The Yellow-rumped Warbler feeds on bayberry during fall migration (Parrish 1997); this shrub was moderately common on Star Island but absent from the Appledore Island plots. The other two species, Cedar Waxwing and Purple Finch, were two of the four highly frugivorous species present in the fall (Table 4). Additionally, the Yellow-breasted Chat was both highly frugivorous and a scrub-shrub breeder, and was also more numerous on Star Island.

Both vegetation structure and species composition can affect habitat suitability and use (Rice et al. 1984, Moore et al. 1995, Finch and Wang 2000). There were differences in plant species and

TABLE 3. Differences in vegetation physiognomy between Star Island and Appledore Island based on a Mann-Whitney *U*-test of means in each category; df = 1 for all tests. There were three plots (0.04 ha) on Star Island and five plots on Appledore Island. Data collected in 2000.

	Star Island		Appledore Island			
Category	# stems	Mean/plot ± SD	# stems	Mean/plot ± SD	*U*	*P*
Live trees						
Density	358	119.3 ± 95.30	986	197.2 ± 36.69	10.00	0.456
Height[a] (m)		3.1 ± 0.48		4.3 ± 0.44	15.00	0.025
Dbh[a] (cm)		4.4 ± 0.44		5.4 ± 0.71	14.00	0.053
Dead trees	13	4.3 ± 2.08	120	24.0 ± 14.05	15.00	0.025
Live shrubs						
Density	3,139	1,046.3 ± 80.71	1,341	268.2 ± 132.14	0.00	0.025
Height[a] (m)		1.3 ± 0.27		1.5 ± 0.23	11.00	0.297
Dead shrubs	919	306.3 ± 231.65	437	87.4 ± 65.89	2.00	0.101

[a] Mean per plot for each island was calculated from means of each individual plot on that island.

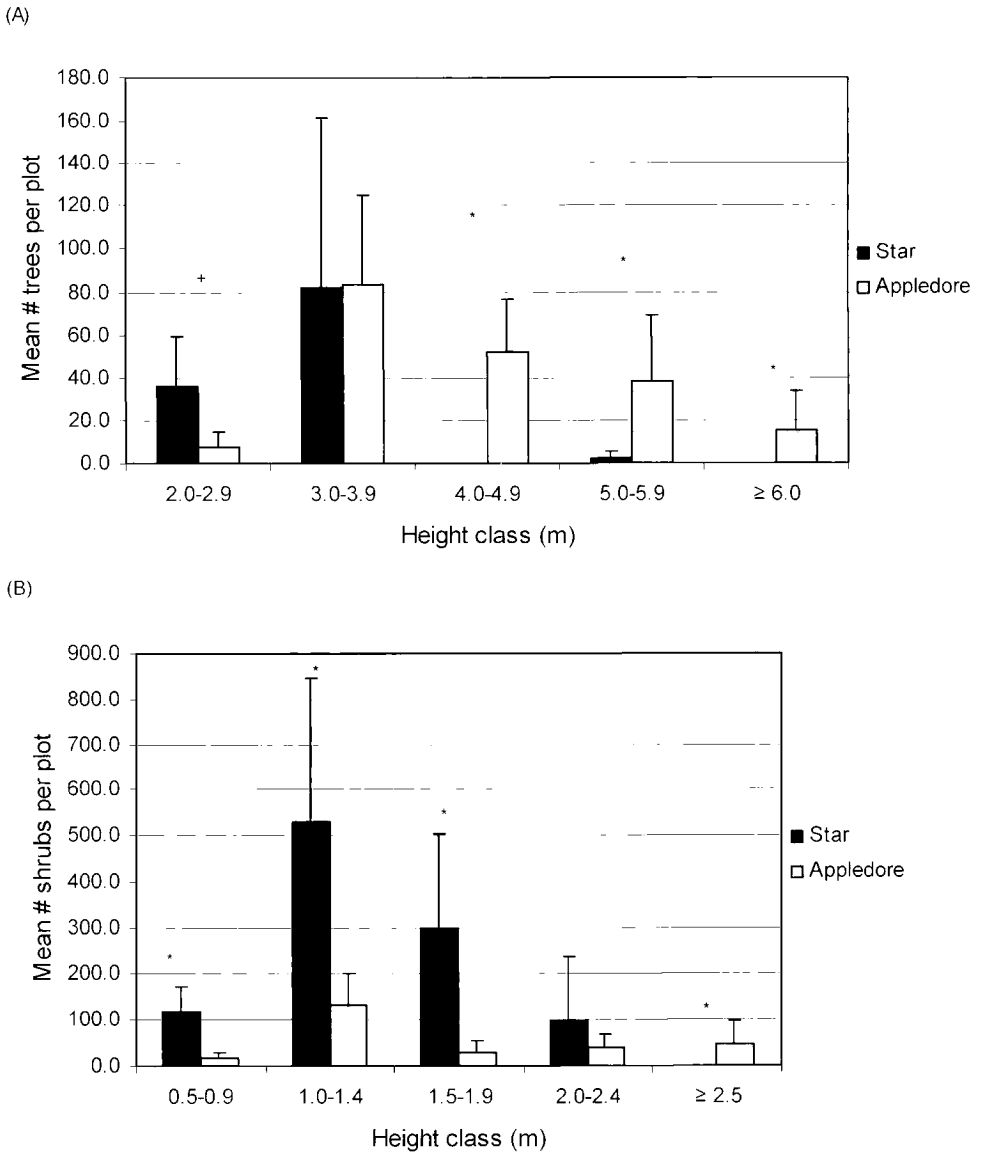

FIG. 1. Distribution of (A) trees and (B) shrubs by height class on Star Island, New Hampshire, and Appledore Island, Maine, in 2000. Bars are means ± SD; * = $P < 0.05$, and + = $0.05 < P < 0.10$.

vegetation structure between islands; the relative importance of these two factors is difficult to assess (Rice et al. 1984). Such was the case with Yellow-rumped Warbler, which feeds on bayberry during fall migration (Parrish 1997) and was more common on Star Island, the only island where bayberry occurred. However, the effect of habitat structure cannot be distinguished from the presence of bayberry (Kwit et al. 2004). The primary factor is likely structural differences for most species because migrants must adapt to a wide variety of plant species along their migration route, and species differences between islands were primarily based on breeding habitat structure.

Seasonal shifts in habitat have been observed at other sites (Winker et al. 1992, Weisbrod et al. 1993, Wang et al. 1998), but only Blue-headed Vireo in our study had a seasonal switch between islands. Thus, most species in this study were captured more frequently on the same island

TABLE 4. Ecological classifications for each avian species. SI = Star Island, AP = Appledore Island, – = no difference between islands, and blank = species not present in sufficient numbers to analyze. Area sensitivity without parentheses is from Robbins et al. (1989); in parentheses is from individual species accounts in The Birds of North America.

Species	More captures spr/fall	Area sensitivity (breeding)	Breeding habitat			Frugivory (fall)[c]
			General category[a]	Veg type[b]	Special characteristics	
Northern Flicker	/–	No	F-FE	M		
Eastern Wood-Pewee	–/–	No	F-FE	D-M		
Yellow-bellied Flycatcher	–/–	(No)	F-SF	C	Forests and bogs	Medium
Traill's Flycatcher	SI/SI	(No)	SS-FE	D		Med-hi
Least Flycatcher	–/–	(Yes?)	ES-F-FE	D-M		Medium
Eastern Phoebe	/–	(No)	FE	D-M		Med-hi
Blue-headed Vireo	AP/SI	No	F	C-M		Medium
Philadelphia Vireo	/–	(No)	F-FE-ES	D-C-M		Med-hi
Red-eyed Vireo	AP/AP	Yes	F-FE	D-M		Med-hi
Red-breasted Nuthatch	–/–	(No)	F	C-M	Mature forests	
Brown Creeper	/AP	No	F	C-D-M	Mature forests	Low
Golden-crowned Kinglet	/–	(No)	F	C		Low
Ruby-crowned Kinglet	SI/SI	(No)	F	C-M		Low
Veery	–/AP	Yes	F	D	Dense understory	Med-hi
Swainson's Thrush	AP/–	(Yes?)	F-FE-ES	C-M		Med-hi
Cedar Waxwing	SI/SI	No	FE	D	Fruit/berry producers	High
Nashville Warbler	–/–	(No)	ES-F-FE	C-D-M		Medium
Northern Parula	–/–	Yes	F-FE	C-D-M	Mature forests	Medium
Chestnut-sided Warbler	–/–	No	SS-ES-FE	D	Dense low growth	
Magnolia Warbler	SI/SI	No	F-ES	C-M	Dense understory	Med-hi
Black-throated Blue Warbler	AP/AP	Yes	F	D-M	Dense sapling/shrub understory	Medium
Yellow-rumped Warbler	SI/SI	(No)	F	C-M		Med-hi
Black-throated Green Warbler	–/–	No	F	C-M	Mature forests	Medium
Blackburnian Warbler	–/	(No)	F	C-M	Mature forests	
Blackpoll Warbler	–/–	(No)	F-SF	C	Low northern spruce	Medium
Black-and-white Warbler	AP/AP	Yes	F	D-M	Forests with saplings	Low
American Redstart	–/AP	No (Yes?)	ES-F-FE	D	Thick sapling understory	Low
Ovenbird	AP/AP	Yes	F	D-M	Mature forests	Medium
Northern Waterthrush	AP/AP	Yes	F-FE	D	Wetland/pond edges	Med-hi
Mourning Warbler	AP/–	(No)	SS-ES	D-M	Dense saplings/shrubs	Med-hi
Wilson's Warbler	SI/SI	(No)	SS-SF	D		Low
Canada Warbler	AP/–	Yes	F	D-M	Dense understory	Low
Yellow-breasted Chat	/SI	No	SS-FE	D	No overstory	High
Savannah Sparrow	SI/	(No)	O	G		
Lincoln's Sparrow	–/SI	(No)	SS-FE-SF	D-M		Med-hi
Swamp Sparrow	SI/SI	(No)	SS	D-G	Wetlands	Medium
White-throated Sparrow	–/SI	(No)	FE-ES-SF	D-C-M	Brushy understory	Med-hi
Rose-breasted Grosbeak	–/	Yes	FE-F	D		High
Baltimore Oriole	–/–	No	FE	D		
Purple Finch	SI/SI	(No)	F-FE	C-M		High

[a] Habitat categories: ES = early successional, F = forest, FE = forest edge, SF = short forests at high elevation and in bogs, SS = scrub/shrub, and O = open areas, grasslands, emergent wetlands.
[b] Vegetation type (veg type), C = coniferous, D = deciduous, G = grassland/sedge/reed, and M = mixed coniferous-deciduous.
[c] Frugivory based on mean percentage of fruit in fecal samples (Parrish 1997): low 0–29, medium 30–59, medium-high (med-hi) 60–89, high 90–100%, and blank = not in analysis.

during both spring and fall. The consistency of habitat selection by a wide range of migrant species between spring and fall supports the hypothesis that habitat selection in passerines is endogenous (Bairlein 1983, Morton 1990, Winker 1995). Migrant distribution might be expected to change between spring and fall, after the large proportion of young migrants have had more exposure to a variety of habitats on both their southward and return migrations, if habitat

selection was learned. Additionally, the correlation of stopover habitat with breeding habitat indicates innate preferences as suggested by Moore et al. (1995).

The apparent association with breeding habitat by migrants during stopover is consistent with Petit's (2000) analysis of habitat selection in five studies. Smaller physiognomic and plant species differences between islands were associated with differences in species distribution between islands. Our study suggests stopover habitat use was related to habitat structure, plant species, diet (extent of frugivory), and habitat area, but the predominant factor(s) may differ among species.

Habitat differences between these two islands were smaller in structure and species type than described in other stopover habitat studies (e.g., Bairlein 1983, Moore et al. 1990, Rodewald and Brittingham 2004); but differences between islands were associated with differences in bird species distribution. Nocturnal migrants typically land when it is still dark and are unlikely to make stopover decisions based on these small habitat differences. Migrants may conduct habitat exploration flights during the day (Moore and Simons 1992, Wiedner et al. 1992), but few birds banded on one island were recaptured on the other island (Suomala 2005) indicating little movement after initial landing. We suggest several mechanisms to explain the detection of small habitat differences: (1) migrants may be landing at the Isles of Shoals later in the morning than migrants at other locations and are able to see detailed habitat features; (2) migrants may be able to see certain features in the dark; and/or (3) there is a non-visual component of stopover habitat selection, similar to the vocal social cuing that Betts et al. (2008) reported was more important than vegetation structure in habitat choice for breeding site selection.

CONSERVATION IMPLICATIONS

Priority stopover habitat for the bird community may be difficult to define due to differing habitat preferences of individual species (Hutto 2000, this study). Protection of stopover sites with a wide variety of habitats, both forest and scrub-shrub, is important to meet the needs of migrant passerines (Weisbrod et al. 1993, Rodewald and Brittingham 2004, this study).

The species-specific differences in habitat use in this study suggest migrants are not using the Isles of Shoals as simply emergency stops, landing at random out of desperation. Scrub-shrub habitat is naturally occurring on the coastal plain and a good source of berry-producing shrubs, which may be one of the best areas for migrants to deposit fat (Parrish 1997). Other studies have demonstrated the importance of edge and shrubland habitats with fruit to fall migrants (Parrish 1997; Suthers et al. 2000; Rodewald and Brittingham 2002, 2004), but the management of scrub-shrub habitat for migrants may be overlooked as an important priority.

Land use changes along the coast are occurring rapidly with resulting deterioration of stopover habitat (Mabey and Watts 2000). Coastal development creates a landscape that is often inhospitable to migrating birds. Conservation efforts for migrant songbirds should encompass the remaining small patches of natural habitat that may be critical to migrant survival (Blake 1986). Education and local land use policies may be effective tools for maintaining small habitat patches on private lands (Mabey and Watts 2000).

ACKNOWLEDGMENTS

This project was made possible by support from the Star Island Corporation and New Hampshire Audubon, grants from the Eastern Bird Banding Association and the University of New Hampshire Graduate School, and the generous donations of many individuals. This effort would not have been possible without help of volunteers at New Hampshire Audubon, the Star Island banding station, and the Appledore Island Migration Banding Station, supported in part by the Shoals Marine Laboratory. This paper is contribution # 14 of the Appledore Island Migration Banding Station and contribution # 153 of the Shoals Marine Laboratory.

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