

SEASONAL SHIFTS IN POPULATION DISTRIBUTIONS AND HABITAT OCCUPANCY BY PERMANENT RESIDENT FOREST BIRDS IN EASTERN CONNECTICUT

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Abstract. I studied 10 permanent resident bird species in unfragmented forests of eastern Connecticut to discover: 1) are populations of resident species truly sedentary or do they seasonally change in density and distribution and 2) are any seasonal changes in species' occurrences related to environmental parameters in manners that help to explain the changes? I performed duplicate surveys using the variable circular plot technique at 50 systematically placed transects and characterized habitats at 15 plots/ transect. I related population densities to habitat features and also compared the occurrence of individual birds within habitat plots to the characteristics of those plots. The Tufted Titmouse (*Poecile bicolor*), Blue Jay (*Cyanocitta cristata*) and Northern Cardinal (*Cardinalis cardinalis*) showed consistent, significant population declines, whereas the Black-capped Chickadee (*P. atricapillus*) showed significant increases from summer to winter and the Red-bellied Woodpecker (*Melanerpes carolinus*) had nearly significant winter increases. Five species had no clear seasonal trend. Populations of six of 10 species became significantly more concentrated from summer to winter at lower, more southerly elevations. Evidence for the association of species with aspects of habitat structure was limited regardless of the scale used to examine such associations. The lack of strong structural habitat associations may be expected among species often thought of as being ecological generalists, although findings also demonstrated that the importance of structural features was not annually consistent, perhaps because these features varied in their annual importance. Despite observed population shifts by most resident species, including those thought to be largely sedentary, the principal factor related to seasonal population changes was wintering at lower, southerly elevations. Because elevation and latitude are strongly related inversely to average temperature in Connecticut, winter movements are likely driven by populations seeking less metabolically costly landscapes.

Permanent resident bird species are a heterogeneous group that constitutes the majority of winter and some of the most abundant summer inhabitants of northeastern North American forests (Root 1988, Sauer et al. 2008). Despite their abundance in forest communities, patterns in their seasonal population distributions remain largely unquantified below the continental scale (e.g., Sauer et al. 2008) and environmental factors potentially influencing distribution shifts are incompletely studied.

Structural habitat features have been associated with landscape scale patterns of distribution and abundance of resident bird species during summer (Craig et al. 2003) and winter (Pearson 1993), with features such as shrub density (Doherty and Grubb 2000), forest composition (Welsh and Loughheed

1996), tree size and canopy cover (Morrison et al. 1986) influencing species occurrence. Seasonal shifts in habitat occupancy may relate to seasonal redistribution of populations (Craig et al. 2003).

The direct relationship of climate to populations at the landscape scale is unknown, although continent-wide studies have suggested that regional temperature variation influences distributions, particularly in winter (Evans et al. 2006). Root (1988) showed that 40% of North American species have northern range limits that coincide with winter temperature isoclines, and continental patterns in winter species richness are reported to increase to the south with increasing average temperatures to regions that have a maximum of 245 frost-free days (Bock and Lepthien 1974, Evans et al. 2006). These types of relationships are thought to occur because metabolic costs are reduced in milder climates (Wright 1983, Lennon et al. 2000).

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The 10 most widespread forest species in southern New England (Craig et al. 2003) are the Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*P. villosus*), Red-bellied Woodpecker (*Melanerpes carolinus*), Blue Jay (*Cyanocitta cristata*), Black-capped Chickadee (*Poecile atricapillus*), Tufted Titmouse (*P. bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), American Robin (*Turdus migratorius*), Northern Cardinal (*Cardinalis cardinalis*) and American Goldfinch (*Spinus tristis*). Robins (Sallabanks and James 1999), cardinals (Halkin and Linville 1999) and goldfinches (Middleton 1993) are considered non-forest species, but they are common in forest openings and forested wetlands, and goldfinches can be frequent winter inhabitants of even interior forest communities (Craig et al. 2003).

Woodpeckers (Shackelford et al. 2000, Jackson and Ouellet 2002, Jackson et al. 2002), titmice (Grubb and Pravosudov 1994), chickadees (Loery and Nichols 1985, Smith 1993), nuthatches (Pravosudov and Grubb 1993) and cardinals (Halkin and Linville 1999) are reported to be generally sedentary, with movements confined to short-distance juvenile dispersal or irregular winter irruption events. Anecdotal evidence suggests that some individuals also may be more regularly migratory toward northern range limits (Shackelford et al. 2000, Jackson et al. 2002). The actual extent to which these species move is, however, poorly understood (Smith 1991, Jackson et al. 2002). In contrast, jays (Smith 1986, Tarvin and Woolfenden 1999), robins (Sallabanks and James 1999) and goldfinches (Middleton 1993) are well documented, relatively short distance seasonal migrants.

I report here on 10 permanent resident bird species occurring in unfragmented forests of eastern Connecticut to discover the following: 1) are populations of resident species truly sedentary or do they seasonally change in density and distribution and 2) are any seasonal changes in species' occurrences related to environmental parameters in manners that help to explain the changes?

METHODS

Study areas. I chose eastern Connecticut for study because it is primarily forested and exhibits environmental conditions that range from mountainous to coastal. The northern half has steeply hilly topography reaching elevations of 401 m, a mean annual temperature of 8.3°C and latitudes ranging north to 42°02', whereas the southern half has elevations generally below 120 m, ranging to 0 m at the coast, a mean annual temperature of 10.0°C and latitudes ranging south to 41°17' (Brumbach 1965, Dowhan and Craig 1976). A strong, negative linear relationship exists between elevation, latitude and temperature in this region (NOAA 2004). Forest cover varies from 69% in the north to 63% in the

south. Its most widespread forest associations are those dominated by oaks and hickories, although to the north conifer-hardwood associations are present (Alerich 1999, Craig et al. 2003).

I divided eastern Connecticut into northeastern and southeastern portions for surveys, with the boundary between them coincident with ecoregional boundaries defined by Dowhan and Craig (1976). The source pool of study sites was public access parcels. I sampled the two regions systematically with a sampling grid, randomly choosing one study site/grid cell although, in practice, many cells contained only one available choice. In six cells with no sites available (e.g. urban areas), I sampled sites closest to cell boundaries or, in two instances, substituted parcels in regions with ca 90% forest cover to sample more equitably the forests in those regions. Based on the size of the regions and their extent of forest cover, I surveyed 26 unfragmented forests (all at least 200 ha) in northeastern and 24 sites in southeastern Connecticut to provide similar levels of sampling intensity. I surveyed northeastern Connecticut in the summers of 2001 and 2004 and winters of 2001–2002 and 2004–2005, and southeastern Connecticut in the summers of 2002 and 2005 and winter of 2002–2003 and 2005–2006, thereby producing duplicate sets of data that could be used to account for temporal variance in results.

Bird surveys. I used the variable circular plot (VCP) technique to document populations of the 10 most widespread forest species (species occurring at ca. 75% or more of study sites)—those for which statistically defensible conclusions could be drawn. The next most common species, the Brown Creeper (*Certhia americana*), was present at only 50% of study sites, which made attempts at statistical analysis of its occurrence inconclusive. The species surveyed included nearly 70% of all wintering individuals present in the study area.

Routes began at first light (ca. 05:15 in summer, 07:00 in winter) and lasted about 3.5 h. Because observer differences in perception can be great (McDonald 1981, Davis 1981), I made all observations to eliminate this source of variance. I established a line transect at each sampling location, with transects traversing about 3.2–4 km of forest depending upon terrain and other local conditions. Along each transect, I set 15 points (750 total points), the maximum number I could survey during the peak of morning bird activity (before 09:00 in summer and 10:30 in winter), and recorded locations and elevations of points with a Garmin Etrex global positioning device. Survey points were generally about 200 m apart, a distance empirically determined to minimize detecting the same birds from two successive points, and greater than that used in other studies (e.g., Scott et al. 1986). I sampled at each point for eight minutes, a time used frequently in VCP surveys because it is thought to be short enough to approxi-

mate an instantaneous count (minimize movement of birds), yet long enough to record adequately all birds present (DeSante 1981, Scott et al. 1986). At each point, I estimated the horizontal distance at first detection (virtually always aural) to all birds encountered.

Environmental measurements. After each bird survey, I visually evaluated habitat structure in a 70 m radius from each sampling station, verifying and refining these determinations during my at least four visits/ site. To evaluate, I used global positioning to walk a straight line beginning 70 m before to 70 m past a sample point, and observed in all directions to 70 m when at the sample point. I chose to establish much larger study plots than those typically used in forest habitat evaluations (e.g. Alerich 1999) because they sampled at a scale more like that at which the majority of bird species in this study actually used forests. I used U. S. Forest Service (USFS) criteria (Alerich 1999) in estimating to the nearest 10% a) forest type: 1) deciduous: $\leq 10\%$ evergreen conifers, 2) mixed: 20–60% evergreen coniferous, 3) coniferous: $\geq 70\%$ evergreen conifers, and b) vegetation type: 1) oak-dominated (oak, hickory, black birch, *Betula lenta*), 2) mixed deciduous (e.g. red maple, *Acer rubrum*, white ash, *Fraxinus americana*, yellow poplar, *Liriodendron tulipifera*), 3) conifer-hardwood (e.g., eastern hemlock, *Tsuga canadensis*, eastern white pine, *Pinus strobus*, northern red oak, *Quercus rubra*, sugar maple, *A. saccharum*–American beech, *Fagus grandiflora*, yellow birch, *B. alleghaniensis*), 4) pine-oak (e.g., eastern white pine, pitch pine, *P. rigida*, scarlet oak, *Q. coccinea*), 5) conifer (eastern hemlock, eastern white pine, plantation conifers), 6) mixed sites (e.g., half oak-dominated, half mixed deciduous).

My vegetation definitions slightly differed from those of USFS to better reflect forest conditions in the study area. Virtually none of the USFS “northern hardwood” category (beech-birch-maple associations typically found across northern New England) is truly present, so to portray more accurately local forests that were northern-associated, I added the restriction that at least 20% of the forest be composed of conifers. This distinguished such forests from associations found in typically mesic or hydric conditions, such as red maple-sugar maple-yellow birch forests, and more effectively restricted the vegetation type to one in which other typical northern community associates, such as Striped Maple (*A. pensylvanicum*) and Hobblebush (*Viburnum alnifolium*), also were present. I grouped the mesic associations into “elm-ash-maple” forests of USFS, which are also associated with mesic conditions. Moreover, I included associations with a minimum of 20% pine cover, instead of the 25% required by USFS as pine-oak forests, because I found 20% to be closer to the minimum conifer cover typically used by conifer-

associated bird species.

Considering the very large size of study plots, I chose to evaluate additional habitat variables by partitioning into categories the major distinctions in their occurrence (rationale detailed by Craig et al. 2003): c) moisture regime: 1) hydric: poorly drained wetland conditions, 2) mesic: well drained soils with plant communities typical of moist conditions, 3) xeric: exposed bedrock and sandy, gravelly conditions characterized by dry site plant communities; d) prevailing canopy tree dbh: 1) young forest: ≤ 15 cm, 2) mature forest: >15 –45 cm, 3) old growth: > 45 cm; e) canopy cover: 1) open: $\leq 40\%$ canopy cover, 2) semi-open: 50–60% cover, 3) closed: $\geq 70\%$ cover; f) understory density (1–4 m tall): 1) open: $\leq 20\%$ cover, 2) moderate: 30–60% cover, 3) dense: $\geq 70\%$ cover. I used the numeric values listed in analyzing habitat data from plots. Because latitude and elevation are closely related and show a strong relationship to local temperature regimes in Connecticut (Brumbach 1965, NOAA 2004), for each transect I divided elevation by latitude, thereby producing a location variable that scaled the effects of elevation with respect to latitude. This variable better predicted habitat relationships than its components in exploratory analyses.

I assigned plots an intermediate numeric value (e.g. 1.5) when they had intermediate characteristics (e.g. half of a plot was hydric and half mesic). If, however, a plot was comprised of $\geq 70\%$ of a single category, I assigned the plot the value of that category. Although I attempted to approximate random sampling of habitats, producing a truly random sample for a region where most land is in private ownership was impossible. Hence, I compared my observations with independently gathered U.S. Forest Service data on forest vegetation (Alerich 1999) to further evaluate whether my sampling was representative.

Analysis. I evaluated collinearity among elevation/latitude and habitat variables by examining data plots, Pearson correlation matrices and regression collinearity diagnostics with SPSS version 15.0 software (SPSS 2006). Forest and vegetation type proved significantly correlated, so I dropped forest type from further analysis because vegetation type yielded a more detailed view of forest composition. Other variables showed no significant relationship.

I calculated population densities with Distance 5.0 software (Thomas et al. 2006), using field data on detection distances to compute detection functions. Choosing a function was iterative, involving progressive refinements to produce a model that minimized variance and yielded a curve with near 100% detection probability when detection distance was zero. During model selection, I grouped similar distances to minimize data “heaping” and to improve the robustness of density estimations, and I dropped the

largest 5–10% of detection data to eliminate outliers. I explored data fit to models recommended by Buckland et al. (2001) and chose the best fitting model by visual inspection of plotted data, with Akaike's Information Criterion and with chi-square tests. In instances where species occurred in flocks, these (termed clusters by the software) were the basis of density measurement (Buckland et al. 2001). I computed separate detection functions for winter and summer to account for differences in detectability and social organization that occurred between seasons.

Because I duplicated observations in northeastern and southeastern Connecticut, I was able to examine regional differences in light of annual variation in populations. However, most population data were not normally distributed, with particularly winter data tending to have probability distributions skewed toward more low-density populations. To seek evidence for seasonal changes in populations, I performed 20 separate nonparametric Wilcoxon test significance tests, correcting for true α levels with the false discovery rate method (Benjamini and Hochberg 1995). I computed summer-winter differences in populations that were negative when summer values were lowest and positive when they were greatest to determine if populations shifted geographically or changed patterns of occurrence in habitats from summer to winter. Computing in this manner yielded data that met parametric assumptions. I used a repeated measures regression analysis to enter population differences within years as dependent variables and mean transect values of vegetation types (proportionate cover), moisture regime, dbh, canopy cover, understory density and location as independent variables. In this and other tests, I checked the fit to model assumptions with data plots, frequency histograms, residual plots and Kolmogorov-Smirnov normality tests. I considered the significance of effects and η^2 (partial eta²—an estimate of effect size) in assessing test results. In the case of the Downy Woodpecker, I rescaled seasonal differences to all positive values by adding 50 to each before computing a transformation to yield normally distributed data. In the case of the Red-bellied Woodpecker, where data conformed poorly to parametric assumptions, I sought correlations of population with geographic location and habitat structure using the nonparametric Kendall's tau-b statistic, correcting α levels for multiple hypothesis tests with the false discovery rate method.

I also looked for evidence of species-habitat relationships by compiling habitat measures associated with individual birds detected within habitat plots during VCP sampling. Because habitat measures thus derived were largely categorical, I related seasonal occurrences of birds to habitat with stepwise binary logistic regression analysis. I performed analyses on data with a level of precision of $\pm 10\%$ of the

95% confidence interval, which translated to a minimum sample size of 33 observations/season/year, a size similar to that computed by Morrison et al. (1986) for comparable analyses. When analyzing habitat affiliations of flocking species, I used only one observation/flock to preserve statistical independence of observations. Because observations at individual survey points were brief enough so that I could distinguish each individual present and because the distance between sampling stations was ca. 200 m, I assumed that habitat measures obtained were from separate individuals. I evaluated model fit with the Nagelkerke r^2 , Hosmer and Lemeshow goodness of fit test, $-2 \log$ likelihood probability and the percent of observations correctly classified by the model.

RESULTS

When I compared my estimates of USFS vegetation cover with those of Alerich (1999), I found that they were generally within standard error measures of each other. My 750 plots sampled an area of 1154.5 ha in eastern Connecticut, compared with 451 USFS plots covering 30.3 ha for the entire state. Standard error estimates showed that my data had greater precision than those of USFS and, considering my much greater sampling area, likely greater accuracy.

The Tufted Titmouse, Blue Jay and Northern Cardinal showed consistent, significant population declines from summer to winter, averaging 29%, 65% and 49%, respectively. In contrast, the Black-capped Chickadee significantly increased an average of 28% from summer to winter in one and probably both sets of study years, and the Red-bellied Woodpecker showed a nearly significant winter increase that averaged 38% for both sets of years. The remaining five species studied showed little seasonal variation or no consistent trend (Table 1). Despite the declines registered by three species, populations of six of 10 became significantly more concentrated at the lower elevations of southeastern Connecticut from summer to winter although, based on η^2 values, the relationship was modest (Table 2). Moreover, the Red-bellied Woodpecker and Tufted Titmouse tended toward a shift in populations to southeastern Connecticut. Only the Downy and Hairy Woodpeckers showed no clear trend toward population movements. The American Goldfinch also demonstrated a significant temporal change in populations, with summer to winter populations undergoing a decline in 2001–2003 and an increase in 2004–2006 (Table 1,2).

Populations of species showed few significant shifts in seasonal associations with habitats and no shifts occurred during both sets of observations (Table 2). Winter Red-bellied Woodpecker populations increased over those of summer in forests of

more open canopies in 2004–2006. Winter American Goldfinch populations increased over those of summer in more deciduous vegetation (primarily in 2004–2006) and in forests with more closed canopies (primarily in 2001–2003).

Data on individual birds observed within habitat plots showed that location significantly distinguished summer vs. winter occurrence during at least one set of years for four of six species with sufficient data for analysis, and all species showed at least a weak trend toward occurring in winter habitats of lower, southerly elevations (Table 3,4). Moreover, three species exhibited a significant seasonal change in use of vegetation during at least one set of years, with the Tufted Titmouse and American Goldfinch shifting to increasingly deciduous associations and the White-breasted Nuthatch shifting to increasingly coniferous associations from summer to winter (Table 3,4). The Tufted Titmouse also moved into winter habitats with denser understories during one set of years (Table 3, 4). The American Robin was the only species to show no significant habitat shifts. However, despite the occurrence of some significant trends, the strength of observed shifts was in all cases subtle and

variable among years (Table 4).

DISCUSSION

This study demonstrates that species thought to be largely sedentary, including the Tufted Titmouse (Grubb and Pravosudov 1994) and Northern Cardinal (Halkin and Linville 1999), instead undergo winter population declines in eastern Connecticut, whereas the Black-capped Chickadee (Loery and Nichols 1985, Smith 1993) and likely the Red-bellied Woodpecker (Shackelford et al. 2000) undergo population increases. The titmouse and cardinal are more southerly-distributed and were virtually absent from Connecticut before 1950 (Zeranski and Baptist 1990), which suggests that these northernmost populations move south out of the study area rather than experience mortality. In contrast, northern populations of the more northerly-distributed chickadee appear to move into the region, as they previously have been suspected of doing in New England (Smith 1986) and also may do in the Pacific Northwest (Morrison et al. 1986). The weak but consistent increase of the Red-bellied Woodpecker is more problematic, as this species is very near its northern range limit and

TABLE 1. Seasonal densities (birds/ km² ± SD) of permanent resident forest birds with tests of significant seasonal difference corrected for false discovery rate.

Species	Summer		Winter		Wilcoxon test <i>P</i>	
	2001–2003	2004–2006	2001–2003	2004–2006	2001–2003	2004–2006
Red-bellied Woodpecker	1.4±1.4	1.5±1.5	2.3±2.9	2.4±2.7	0.064	0.105
Downy Woodpecker	7.2±5.2	7.9±4.6	7.8±4.5	8.3±4.7	0.318	0.313
Hairy Woodpecker	1.3±1.9	3.0±2.8	2.4±3.1	2.6±2.6	0.470	0.431
Blue Jay	4.0±2.0	3.4±1.8	1.3±1.3	1.3±1.4	<0.001**	<0.001**
Black-capped Chickadee	15.8±7.1	18.1±7.7	20.5±11.7	26.4±10.5	0.027	<0.001**
Tufted Titmouse	25.8±10.6	29.3±11.2	17.2±14.6	21.8±17.5	<0.001**	0.001**
White-breasted Nuthatch	8.3±4.7	7.6±4.2	7.6±4.5	9.1±4.3	0.215	0.049
American Robin	6.5±6.1	8.3±6.8	6.6±9.5	10.4±8.1	0.637	0.077
Northern Cardinal	3.7±3.6	5.3±4.6	1.7±3.4	2.9±4.4	0.001**	0.001**
American Goldfinch	14.4±8.7	14.7±9.0	10.8±11.1	15.8±15.6	0.066	0.958

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TABLE 2. Seasonal population shifts between northeastern and southeastern Connecticut tested with repeated measures regression analysis for significant differences in effects of years, seasons and habitat values. P = probability of no significant difference, η^2 = proportion of variance explained. Red-bellied Woodpecker-Kendall's tau-b probabilities for 2001–2003 and 2004–2006. Significance tests corrected for false discovery rate. * significant, ** highly significant.

	Measure	Years	Years x vegetation	Years x canopy	Years x understory	Years x moisture	Years x elev/ lat	Vegetation	Canopy	Understory	Moisture	Elevation / latitude	
Red-bellied Woodpecker	P P	(2001-3) (2004-6)						0.112 0.401	0.844 0.001**	1.000 0.150	0.766 0.867	0.018 0.021	
Downy Woodpecker	P η^2		0.962 0.000	0.609 0.008	0.555 0.055	0.117 0.003	0.741 0.050	0.137 0.037	0.198 0.010	0.516 0.108	0.026 0.015	0.421 0.005	0.648
Hairy Woodpecker	P η^2		0.219 0.034	0.523 0.009	0.858 0.064	0.091 0.023	0.319 0.003	0.712 0.013	0.457 0.023	0.313 0.007	0.592 0.010	0.506 0.006	0.618
Blue Jay	P η^2		0.603 0.006	0.113 0.056	0.353 0.020	0.340 0.021	0.518 0.010	0.449 0.013	0.104 0.059	0.137 0.049	0.719 0.003	0.462 0.012	0.001** 0.243
Black-capped Chickadee	P η^2	0.034 0.098	0.576 0.007	0.046 0.087	0.530 0.009	0.034 0.098	0.658 0.004	0.994 0.000	0.602 0.006	0.996 0.000	0.056 0.081	0.016* 0.125	
Tufted Titmouse	P η^2		0.634 0.005	0.910 0.000	0.211 0.035	0.976 0.000	0.341 0.021	0.746 0.002	0.358 0.019	0.170 0.042	0.766 0.002	0.281 0.026	0.181 0.040
White-breasted Nuthatch	P η^2	0.953	0.894 0.000	0.864 0.000	0.412 0.001	0.752 0.015	0.081 0.002	0.456 0.068	0.149 0.013	0.656 0.047	0.405 0.005	0.017* 0.016	0.122
American Robin	P η^2		0.836 0.001	0.981 0.000	0.651 0.005	0.334 0.021	0.069 0.073	0.407 0.016	0.730 0.003	0.270 0.028	0.149 0.047	0.498 0.011	0.007** 0.153
Northern Cardinal	P η^2		0.346 0.020	0.029 0.104	0.747 0.002	0.155 0.045	0.887 0.000	0.410 0.015	0.053 0.082	0.111 0.057	0.427 0.014	0.804 0.001	0.016* 0.125
American Goldfinch	P η^2		0.001** 0.237	<0.001** 0.250	0.005** 0.169	0.041 0.091	0.603 0.006	0.881 0.001	0.070 0.073	0.399 0.016	0.565 0.008	0.598 0.006	<0.000** 0.249

might also be expected to decline as birds leave the region in winter, as they may do in Michigan (McPeck and Pitcher 1991). The fact that the species tends to concentrate in southeastern Connecticut likely indicates that the small population to the north joins northern Connecticut birds in wintering there, producing a small but detectable increase.

That winter populations of eight of 10 species also exhibit at least trends toward concentrating in lower elevation, southeastern Connecticut further

suggests seasonal movements by most residents. Observations that species tend to occur more frequently in winter habitat plots of lower, southerly elevations corroborates this. Moreover, incidental but annually consistent observations made at the study sites in March, the local beginning of spring migration, show increases in titmice and chickadees over their winter numbers (pers. obs.), providing still additional evidence for migration by these species. Because elevation and latitude are strongly related

TABLE 3. Mean seasonal ranks of habitat features (\pm SD) used by individuals of permanent resident species. Vegetation type: 1) oak-dominated – 5) coniferous; moisture regime: 1) xeric – 3) hydric; dbh: 1) < 15 cm – 3) > 45 cm; canopy cover: 1) open – 3) closed; understory density: 1) open – 3) dense; location: 7.50 = maximum, –0.55 = minimum.

Species (total <i>n</i>)	Vegetation type	Moisture regime	dbh	Canopy cover	Understory density	Elevation/ latitude
Downy Woodpecker						
Summer (123)	2.14 \pm 1.62	2.35 \pm 0.67	2.00 \pm 0.11	2.59 \pm 0.53	2.35 \pm 0.60	3.77 \pm 1.90
Winter (143)	2.24 \pm 1.73	2.25 \pm 0.49	2.01 \pm 0.17	2.59 \pm 0.53	2.38 \pm 0.61	3.31 \pm 1.89
Black-capped Chickadee						
Summer (201)	2.53 \pm 1.82	2.22 \pm 0.49	2.01 \pm 0.18	2.59 \pm 0.55	2.32 \pm 0.62	3.78 \pm 1.83
Winter (248)	2.78 \pm 1.93	2.22 \pm 0.51	2.00 \pm 0.20	2.56 \pm 0.53	2.26 \pm 0.63	3.38 \pm 1.82
Tufted Titmouse						
Summer (343)	2.24 \pm 1.72	2.22 \pm 0.50	2.01 \pm 0.15	2.71 \pm 0.47	2.28 \pm 0.63	3.38 \pm 1.80
Winter (211)	2.18 \pm 1.80	2.26 \pm 0.50	1.99 \pm 0.17	2.55 \pm 0.54	2.40 \pm 0.60	2.88 \pm 1.78
White-breasted Nuthatch						
Summer (126)	1.80 \pm 1.34	2.25 \pm 0.58	2.00 \pm 0.45	2.69 \pm 0.48	2.21 \pm 0.60	3.66 \pm 1.88
Winter (131)	2.44 \pm 1.75	2.22 \pm 0.51	2.01 \pm 0.14	2.63 \pm 0.54	2.26 \pm 0.58	3.56 \pm 1.90
American Robin						
Summer (117)	2.54 \pm 1.93	2.14 \pm 0.48	2.00 \pm 0.20	2.52 \pm 0.54	2.29 \pm 0.64	3.30 \pm 1.82
Winter (94)	2.47 \pm 1.99	2.30 \pm 0.55	1.99 \pm 0.16	2.45 \pm 0.60	2.54 \pm 0.56	2.91 \pm 1.58
American Goldfinch						
Summer (230)	2.66 \pm 1.97	2.27 \pm 0.49	1.99 \pm 0.15	2.59 \pm 0.53	2.33 \pm 0.61	3.44 \pm 1.97
Winter (177)	2.08 \pm 1.68	2.25 \pm 0.50	1.99 \pm 0.13	2.55 \pm 0.56	2.32 \pm 0.65	2.46 \pm 1.34

inversely to average temperature in Connecticut (Brumbach 1965, NOAA 2004), southerly movements are likely driven by populations seeking less metabolically costly landscapes during winter (Bock and Lepthein 1974, Root 1988, Evans et al. 2006). At present, there is no evidence that other factors like winter food also increase over the same gradient.

The weaker and largely non-significant evidence for movements by Downy and Hairy woodpeckers is, in contrast, consistent with the tendency of many populations of these species to remain in the same vicinity year-round (Gordon and Confer 1996, Jackson et al. 2002). Indeed, I frequently observed pairs of these woodpeckers present at approximately the same locations both winter and summer. Although northern populations may undergo seasonal movements (Jackson et al. 2002), and have been anecdotally reported to do so in Connecticut (Smith and Devine 1994) and Long Island (Bull 1974), this does not appear to be the case in the study area, unless an influx of northern birds simply offsets an exodus of a portion of the local population.

Despite observed population movements, evidence for the association of species with aspects of forest habitat structure is limited regardless of the scale employed to seek such associations. The most frequently noted findings were the tendency for two species to move to more deciduous environments during winter and for two species to occupy forests of seasonally differing canopy covers. The lack of strong structural habitat associations may be expected among species often thought of as being ecological generalists (e.g., Smith 1991, Shackelford et al. 2000), although my findings also demonstrate that structural features may vary in their annual influence, perhaps because potentially related variables like food availability also vary inconsistently. Still other annual sources of variance, like changes in continental-wide populations, may further exacerbate locally inconsistent shifts in habitat associations.

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TABLE 4. Habitat variables identified by binary logistic regression to shift seasonally in frequency of use by individual birds observed in habitat plots (significance tests corrected for false discovery rate). Nagelkerke r^2 indicates the strength of the relationship between the habitat variables and observations, whereas % correctly classified indicates the percentage of all observations that the regression correctly relates to the habitat variables. * significant, ** highly significant.

Species	<i>n</i>	Variables entered		Nagelkerke r^2 / % correctly classified	-2 log likelihood <i>P</i>		
		into logistic regression			2001–2003	2004–2006	2001–2003
Downy Woodpecker	121/ 145	none	location		0.081 / 57.9		0.003**
Black-capped Chickadee	182/ 267	location	none		0.074 / 57.7	0.001**	
Tufted Titmouse	233/ 321	location understory	vegetation		0.127 / 65.7	0.068 / 64.5	0.003** 0.006**
White-breasted Nuthatch	94/ 163	none	vegetation		0.106 / 61.3		0.019**
American Robin	79/ 132	none	none				
American Goldfinch	126/ 281	location	location		0.348 / 68.3	0.069 / 56.9	<0.001** <0.001**
		vegetation				0.011*	

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