

Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine, USA

Richard M. DeGraaf ^{a,*}, Jay B. Hestbeck ^b, Mariko Yamasaki ^c

^a USDA Forest Service, Northeastern Forest Experiment Station, University of Massachusetts, Amherst, MA 01003, USA

^b Massachusetts Cooperative Fish and Wildlife Research Unit, Holdsworth Hall, University of Massachusetts, Amherst, MA 01003, USA

^c USDA Forest Service, Northeastern Forest Experiment Station, P.O. Box 640, Durham, NH 03824, USA

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Abstract

Assessment of faunal distribution in relation to landscape features is becoming increasingly popular. Technological advances in remote sensing have encouraged regional analyses of the distributions of terrestrial vertebrates. Comparisons of the strength of association of habitat characteristics at various scales of measurement of habitat structure are rare. We compared the associations of forest cover-type, stand size-class, and stand structure to abundance of breeding bird species in managed forest in northern New England. We surveyed breeding birds and measured stand structure in 20 stands to test the hypothesis that forest cover-type, stand size-class, and structure variables were equally associated with numbers of forest birds. We fit regression models to data from each data source to predict the log number of individuals for each species. We restricted our analyses to cover-types with > 1 size-class and to size-classes representing > 1 cover-type, and restricted our comparisons to bird species with at least 10 observations/yr for 2 yr. Of 31 bird species that met our criteria for analysis, a significant ($P < 0.05$) association was detected between bird abundance and structure data for 30 species, cover-type data for 19 species, and size-class data for 10 species. Stand structure was the best predictor of bird abundance for 25 species, cover-type for 5 species, and size-class for none. Of the 14 structure variables used in the analyses, total foliage volume of large and mid-size deciduous trees, density of mid-size trees, total woody stem density, total deciduous understory volume and total volume of large conifers were most frequently important in explaining variation in species abundances. Although each species had a unique set of structural affinities, multi-layered stands are apparently more important to long-distance migrants, in general, than to resident/short distance migrants. Large-scale efforts to identify important habitats, assess degree of protection, or monitor species/habitat trends are important to conservation. For forest birds, such efforts must include estimates of the factors to which the species of concern respond. At the stand scale in New England, it seems that bird abundance is more strongly associated with forest structure than with forest cover-type or stand size-class. © 1998 Elsevier Science B.V.

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* Corresponding author.

1. Introduction

Wildlife habitat relationships are best known at the stand level, i.e., for tree communities of sufficiently uniform age or composition to be distinguishable from other communities, and so constituting silvicultural or management units (Eyre, 1980). Stands are the units that are treated in forest management. On national forests and most industrial forests, management units are inventoried and monitored by forest cover-type and size-class, and often an estimate of density is used to describe the stocking of trees by size-class. Lands are managed to produce planned distributions of forest cover-types and stand size-classes. Cover-type—classification of forest land based on present occupancy by tree species—and size-class—classification of even-aged stands by mean stem diameter—are readily obtained and mapped from forest inventories. The relationships between occurrence of wildlife species and forest cover-types and stand size-classes have been developed, largely from combinations of exhaustive literature reviews and field surveys, for several regions of the United States, e.g., New England (DeGraaf and Rudis, 1986), California (Verner and Boss, 1980), and the Pacific Northwest (Thomas, 1979; Brown, 1985). Recently, published associations of vertebrates with mapped or remotely-sensed vegetation cover-types have been used as the bases of landscape approaches to protection of biological diversity (e.g., Scott et al., 1993). How closely are wildlife species associated with forest cover-type, size-class, or stand structure?

Many studies have been conducted on the associations of birds with habitats along environmental gradients (e.g., Bond, 1957; James, 1971; Smith, 1977), among successional stages (e.g., Shugart and James, 1973; Smith, 1982). Most of these studies have shown strong correlations between bird species and habitat features, especially vegetation structure (MacArthur and MacArthur, 1961; James, 1971; James and Wamer, 1982, see also Sherry and Holmes, 1985 and Holmes, 1990 for reviews). Cover-types, although they are collections of ‘snapshot’ descriptions of tree species composition in stands or larger areas, can be readily identified and delineated from aerial photographs. Stand size-classes, which describe in a general way the average estimate of tree

diameter throughout even-aged stands, can be inventoried from forest records if ground plot data are available. However, most studies of habitat selection, especially among forest birds, have used other vegetation characteristics to describe habitats, such as ground cover, understory and overstory height or density, number of snags, tree species composition, or canopy closure.

Recent debate suggests the need to identify the relative strengths of cover-type, size-class, or stand structure as predictors of vertebrate abundance and diversity (e.g., Short and Hestbeck, 1995; Scott et al., 1996). Vegetation structure is generally considered to be the most important proximate factor affecting habitat selection by temperate forest birds (e.g., Hilden, 1965; Willson, 1974). The evolution of habitat preferences is determined by, and determines, a bird species morphology and behavior, in essence its ability to survive in the habitat (Cody, 1985). The diversity of deciduous forest birds in the breeding season is associated with habitat patchiness or horizontal diversity (Roth, 1976) and stand structure or vertical diversity (MacArthur and MacArthur, 1961; Helle, 1985). The notion that birds select breeding habitats in response to structural aspects of the vegetation that they do not actually require for survival was first proposed by Lack (1933). Many studies have attempted to identify the features or patterns sought by various bird species (e.g., Anderson and Shugart, 1974; James, 1971; Titterton et al., 1979). Resource partitioning (niche separation) through habitat selection allows breeding birds of different species to coexist in temperate forests (e.g., Svardson, 1949; Shugart and Patten, 1972; Whitmore, 1977). The set of resources partitioned along gradients related to forest structure is referred to as the habitat niche, and is likely unique to each bird species (see Cody, 1974, 1975; Mengel, 1964). It is likely that these sets of structural habitat features or components are perceived by forest birds when they select breeding habitats (Lack, 1971; Cody, 1985).

Some forest bird species are more sensitive than others to differences in vegetation composition and structure, and their sensitivity may vary with the vegetation attribute under consideration (Morse, 1985). In a spruce–fir (*Picea–Abies*) sere in Maine, magnolia warbler (*Dendroica magnolia*) was the only warbler that occupied all habitats ranging from

recent clear-cuts to mature forest, although abundance differed greatly (Titterton et al., 1979); however, it occupied only 2 of 6 forest cover-types studied in Wisconsin (Beals, 1960). The magnolia warbler shows broad tolerance for size-class and narrow tolerance for cover-type. The ovenbird (*Seiurus aurocapillus*), on the other hand, occupied all Wisconsin cover-types (Beals, 1960) but only the 2 most mature stand conditions in the Maine spruce–fir sere (Titterton et al., 1979).

Another species, black-throated green warbler (*Dendroica virens*), was not responsive to either cover-type or size-class in both of the above studies, but rather was sensitive to forest patch size, and did not occupy small habitat islands that are normally occupied by northern parula (*Parula americana*) and yellow-rumped warbler (*Dendroica petechia*) (Morse, 1971, 1977).

Although a species can tolerate a range of conditions within a forest cover-type, its abundance may vary in response to stand structure. The direction and magnitude of the numeric response to stand conditions varies among bird species. Some species prefer intermediate stocking levels, e.g., yellow-rumped warbler became more abundant when the overstory was reduced in Lake States pine forests (Apfelbaum and Haney, 1981). In the same Lake States pine forests densities of bay-breasted—(*Dendroica castanea*) and blackburnian warbler (*Dendroica fusca*) declined 25% and 50%, respectively, after the canopy was reduced to one-half its previous cover (Apfelbaum and Haney, 1981).

Clearly, forest bird species vary in sensitivity to specific vegetation characteristics. Forest bird communities seem to be more sensitive to changes in forest cover-type and size-class (Morse, 1985) than to within-stand changes that do not greatly alter size-class or cover-type (Webb et al., 1977). Particular species, however, show changes in abundance that are correlated with changes in structure as stands mature. For example, least flycatcher (*Empidonax minimus*) and wood thrush (*Hylocichla mustelina*) abundances changed quite late in the successional sequence in New Hampshire northern hardwood forest (Holmes et al., 1986; Holmes and Sherry, 1988).

Obviously, many habitat features that affect forest bird diversity can be manipulated by forest management. Different species specialize on different forest

attributes—some on habitat type, others on foraging sites, over a wide range of habitat types. The close relationship between habitat structure and bird species composition (compared to other vertebrates) is useful for assessing the effects of forest management on breeding birds at landscape or multi-stand scales. The breeding bird compositions of successional New England northern hardwood stands have been described; four habitat types: regenerating, sapling, pole, and mature, have different breeding bird compositions (DeGraaf, 1987). No unique assemblages of breeding birds are evident at the interfaces of even-aged northern hardwood stands, and effects of boundaries between even-aged stands on breeding birds are ephemeral (DeGraaf, 1992).

We estimated forest cover-type, stand size-class, and within-stand habitat structure associations with breeding birds among 8 forest cover-types and 4 size-classes in the White Mountains of New Hampshire and Maine. The objectives were to compare the ability of cover-type, size-class, or stand structure to predict the abundances of breeding birds. These aspects of forest habitats are important to forest resource managers; while various silvicultural treatments can be used to produce stands of a certain type or crop trees in a certain time period, treatments differ in their abilities to produce structural features that are important to forest birds

2. Study area

This study was conducted on the White Mountain National Forest (WMNF) in New Hampshire and Maine (44°N, 71°W). The WMNF covers 304,000 ha and is located within an extensively forested region, most of which was logged in the late 19th century (Belcher, 1980). Afterwards, extensive fires, fueled by logging debris, burned throughout the region, resulting in the extensive, 90-yr-old, even-aged forest present at the time of the study. WMNF was established in 1918 and has been managed since the 1940s. Sawtimber stands (all types) presently constitute 65% of WMNF, poletimber stands 25%, and younger stands 10% (WMNF records). At higher elevations, red spruce (*Picea rubra*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*) stands predominate; on lower slopes stands

contain sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*), often with components of white spruce (*Picea glauca*), red spruce, balsam fir, eastern hemlock (*Tsuga canadensis*), aspen (*Populus* spp.), and white ash (*Fraxinus americana*) on suitable sites. Valley bottoms support extensive stands of red spruce, white spruce, and balsam fir with associated alders (*Alnus* spp.) and aspens.

Eleven forest cover-types have been delineated on WMNF; 8 cover-types were represented by > 1 size-class, and were included in this study. The sugar maple–beech–yellow birch type (46% of WMNF) is composed of sugar maple, beech, and yellow birch in varying proportions and occurs widely in northern New England. These species comprise the basic hardwood type in northern New England, and occur to an elevation of 760 m on fertile, moist loamy soils. On drier sites, beech becomes more prominent. On wetter sites, the proportions of red maple and yellow birch increase, and beech is absent. Striped maple (*Acer pensylvanicum*) and hobblebush (*Viburnum alnifolium*) are common in the understory throughout the study area (Eyre, 1980).

The red spruce–balsam fir type (5%) consists either of red spruce and balsam fir in approximately equal proportions or together they predominate in a mixture of associates—the composition varies depending on site and disturbance history. This type occupies moderately to poorly drained flats and well-drained to dry, shallow soils on steep, rocky, upper mountain slopes. Associates are red maple, paper and yellow birch, and aspens, white pine, eastern hemlock, and occasionally black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Stands are usually dense; the ground is generally devoid of plants except for mosses or scattered seedlings of red spruce and balsam fir (Eyre, 1980).

The paper birch type (5%) is a pioneer type that follows fire or clearcutting. Common associates are aspens, pin cherry (*Prunus pensylvanica*), northern red oak (*Quercus rubra*), and eastern white pine. The type grows best on deep well-drained soils, but occurs to the subalpine zone in the White Mountains. It is succeeded by northern hardwoods to the south and by spruce-fir and pine types to the north. Beaked hazel (*Corylus cornuta*) and wild lily-of-the-valley

(*Maianthemum canadense*) are common under paper birch stands (Eyre, 1980).

In the swamp hardwood (red maple) type (3%), red maple is dominant or codominant; associates are yellow birch, balsam fir, and sugar maple. The type occupies moist to wet muck or peat soils in swamps, depressions of slow drainage, or along sluggish streams. It can be differentiated readily from northern hardwoods by the absence of beech and the increased proportion of yellow birch and red spruce (Eyre, 1980).

The eastern white pine type (2%) is associated with pitch pine (*Picea rigida*), aspen, red maple, and white oak (*Quercus alba*) on light-textured soils; on heavier soils, associates are birches, white ash, northern red oak, sugar maple, eastern hemlock, balsam fir and red spruce. The type commonly pioneers on abandoned (usually impoverished) agricultural land in New England. The type approaches permanence on drier soils, but is succeeded by hardwoods on heavier soils. Common lady-slipper (*Cypripedium acaule*) is a common herb on dry sites; highbush blueberry (*Vaccinium corymbosum*) is a common understory shrub on wetter sites (Eyre, 1980).

In the balsam fir type (2%), balsam fir is either pure or predominant and occurs on moist or wet-site soils. Common associates on the study area are paper birch, aspens, and northern white-cedar (*Thuja occidentalis*). The type occurs on moderately well-drained to poorly drained flats and in swamps. Pure stands commonly result from heavy cutting or blow-down (Eyre, 1980).

The aspen type (1%) is transcontinental in distribution, and includes quaking (*P. tremuloides*) and bigtooth (*P. grandidentata*) aspen. The type is found on all but the driest and wettest sites. Almost all stands regenerate from suckers. Aspen stands are short-lived, and are replaced by red maple or oaks on dry sites, by white pine in intermediate sites, and by northern hardwoods on fertile sites. Undergrowth is mostly composed of species whose underground parts are able to survive fire (Eyre, 1980).

The eastern hemlock type (1%), as it occurs on WMNF, consists of pure stands or stands with scattered red maples. Hemlock is extremely tolerant, long-lived, and able to respond to release after centuries of suppression. Undergrowth in mature hem-

lock stands is very sparse due to low light levels. Common herbs are wild lily-of-the-valley, bunchberry, and wild sarsaparilla (*Aralia nudicaulis*) (Eyre, 1980).

Four size-classes were used in this study. Sapling stands were 2.5–12.5 cm dbh. Poletimber stands were 12.5–22.5 cm dbh for softwoods and 12.5–27.5 for hardwoods. Sawtimber stands were > 22.5 cm and > 27.5 cm dbh for softwoods and hardwoods, respectively. Large sawtimber stands were > 60 cm dbh.

3. Methods

We surveyed breeding birds and measured structural aspects in 20 stands selected from WMNF records. We surveyed representative stands of all available timber size-classes of 8 forest cover-types that were at least 16 ha and that could contain a 500 m transect > 100 m from the stand boundaries.

3.1. Bird surveys

Skilled observers surveyed breeding birds at the same locations from June 1–30, 1979 and 1980. All surveys were conducted between 0430–0830 on clear, calm mornings. Birds were counted at 5 points 100 m apart along permanent transects through each stand. The numbers of singing or calling males of each species detected within 50 m of survey points were recorded during a 5-min period. All points were surveyed 3 times/yr. The order in which transects were surveyed was chosen randomly each day to equalize detectability of species that sang early or late in the sample period. Bird counts by species were summed over the 5-point transects and over the 3 time periods for each year. We used this total as our measure of abundance for each species in each stand in each year. Totals from each year were used as replicates.

3.2. Vegetation measurement

Structural characteristics of the vegetation were measured at 2 randomly-chosen bird survey points from the 5 points in each stand. The height, crown width, and diameter at breast height of all trees > 10 cm in diameter were measured with a Haga altimeter,

range poles and tape, and diameter tape, respectively, on 0.04 ha circular plots concentric with bird survey points. Basal areas (BA) were calculated. Canopy closure (%) was estimated with a spherical densiometer along N–S and E–W diameters of the plot; 10 measurements at 2 m intervals/diameter were averaged for the mean value at each point. Ground cover (%) was estimated with a sighting tube 15 cm long and 2 cm inside diameter and fitted with crosshairs. Readings were taken at 10 2 m intervals on each N–S and E–W plot diameters. The number of snags—dead trees > 10 cm dbh > 5 m tall—were counted. Heights, crown widths, diameter, and number of woody stems 2–10 cm in diameter and < 2 cm diameter were counted on 4 circular 0.01 ha plots located 20 m from the bird survey point at cardinal directions.

Total crown volumes of foliage from the samples were estimated for coniferous and deciduous trees which were > 10 cm dbh and between 2 and 10 cm dbh using the crown heights and diameters. A total sum of heights of coniferous and deciduous stems was used as a measure of foliage volume for each stem-size group.

We tested the hypothesis that forest cover-type, stand size-class, and structure data equally predict $\log_{10}$ numbers of forest birds for the given stands. We fit separate regression models to data from each classification scheme (cover-type, size-class, or stand structure) to predict the log number of individuals for each species (SAS Institute, 1988). The classification scheme that accounted for the greatest variation in log number of a species, using the adjusted r^2 , was considered to be the best predictor for that species; r^2 is an indicator of how much variation in log numbers is explained for a given species by a particular model. The adjusted r^2 is an alternative to r^2 that adjusts r^2 for the number of parameters in the model and provides a better estimator of explained variation than r^2 when the number of parameters approaches the sample size (SAS Institute, 1988). We restricted our analyses to cover-types with > 1 size-class and to size-classes with > 1 cover-type. This resulted in our eliminating three cover-types that occur on WMNF: red spruce, northern red oak, and oak–pine, and two size-classes: seedling and uneven-aged. We further restricted our comparisons to bird species with at least 10 observations in

each year to ensure that characteristic habitats would be occupied.

The analyses for cover-type used aspen, birch, northern hardwood, swamp hardwood, balsam fir, pine, spruce fir, and hemlock as dummy variables in the regression model with the northern hardwood cover-type as the reference variable. The analyses for size-class used sapling, poletimber, sawtimber, and large sawtimber as dummy variables in the regression model with the sawtimber size-class as the reference variable.

The analyses for structure used 14 vegetation measures as continuous variables in the regression model using the MAXR option (SAS Institute, 1988). The MAXR option, maximum r^2 improvement, finds the best one-variable model, the best 2-variable model, etc., up to the only 14 variable model which includes all available information. We then used the adjusted r^2 and C_p statistic to select the best predictive model.

The variables used to estimate stand structure were:

ACLOS	arcsine transform of canopy closure
GCV	percent ground cover
LNLC	log number of coniferous trees per ha that were > 10 cm dbh
LNLD	log number of deciduous trees per ha that were > 10 cm dbh
LNMC	log number of coniferous trees per ha that were between 2 and 10 cm dbh
LNMD	log number of deciduous trees per ha that were between 2 and 10 cm dbh
LNST	log number of woody stems per ha
LNSNAG	log number of dead trees per ha that were > 10 cm dbh and > 5 m tall
LVLC	log total foliage volume of coniferous trees that were > 10 cm dbh
LVLDD	log total foliage volume of deciduous trees that were > 10 cm dbh
LVMC	log total foliage volume of coniferous trees between 2 and 10 cm dbh
LVMD	log total foliage volume of deciduous trees between 2 and 10 cm dbh
LVSC	log total foliage volume of coniferous stems that were < 2 cm dbh
LVSD	log total foliage volume of deciduous stems that were < 2 cm dbh

4. Results

A total of 76 breeding bird species was observed over all forest cover-types (Appendix A). Of these, 63 occurred in hardwood cover-types, and 65 occurred in softwood cover-types. Thirty-one species were observed at least 10 times/yr. Of these 31 species, a significant ($P < 0.05$) amount of variation in abundance was explained for 30 species using structure data, 19 species using cover-type data, and 10 species using size-class data (Table 1). No classification scheme explained significant variation for the hermit thrush. Stand structure was the best predictor for 25 species, cover-type was best for 5 species, and size-class was best for none. The mean adjusted r^2 values for the 31 species was 0.40 for structure, 0.23 for cover-type, and 0.09 for size-class.

4.1. Cover-type associations

Of the 19 species for which cover-type was significant, the expected log number was non-zero for northern hardwood for all 19 species; for white pine and eastern hemlock for 18 species, for spruce-fir for 17 species, for paper birch, swamp hardwoods, and balsam fir for 15 species, and for aspen for 14 species (Table 2). The magnitude of the expected log number can be used as a measure of importance of each cover-type to explain the variation in log abundance for each species. We counted the number of times that each cover-type was among the 2 highest expected values for each species and used the total as a measure of overall importance of each cover-type. White pine occurred for 10 species, aspen for 6 species, paper birch for 5 species, balsam fir, spruce-fir, and eastern hemlock for 4 species, northern hardwoods for 3 species, and swamp hardwood for 2 species.

Our species' models vary in the degree to which they reflect known or reported habitat associations such as those presented in The Audubon Society Field Guide to North American Birds, Eastern Region (Bull and Farrand, 1977). Our model associates the least flycatcher primarily with paper birch and northern hardwood cover-types. Bull and Farrand (1977) (p. 663) listed the least flycatcher as a bird of deciduous forest. Likewise, the model for rose-breasted grosbeak (*Pheucticus ludovicianus*) indicates that it is associated primarily with aspen and

Table 1

Adjusted r^2 with associated probability of null model for regression models comparing the ability of forest cover-type, stand size-class, and measures of stand structure to predict the log number of breeding birds in the White Mountains, New Hampshire, and Maine, USA

Species	Cover-type		Size-class		Structure	
	A- r^2	P	A- r^2	P	A- r^2	P
Yellow-bellied sapsucker	0.056	0.268	0.056	0.172	0.228	0.022
Eastern wood-pewee	0.086	0.196	0.235	0.005	0.556	< 0.001
Least flycatcher	0.231	0.027	0.081	0.111	0.720	< 0.001
Blue jay	0.152	0.086	< 0.000	0.573	0.236	0.019
Black-capped chickadee	0.039	0.317	0.072	0.130	0.259	0.012
Red-breasted nuthatch	0.494	< 0.001	< 0.000	0.586	0.625	< 0.001
Winter wren	0.317	0.006	0.088	0.099	0.401	0.001
Golden-crown kinglet	0.284	0.011	< 0.000	0.614	0.360	0.004
Veery	0.078	0.213	0.013	0.337	0.261	0.041
Swainson's thrush	0.092	0.183	0.003	0.388	0.362	0.002
Hermit thrush	0.003	0.437	< 0.000	0.488	0.129	0.116
Wood thrush	< 0.000	0.929	0.049	0.190	0.294	0.026
Solitary vireo	0.076	0.218	0.108	0.069	0.157	0.040
Red-eyed vireo	0.465	< 0.001	0.055	0.172	0.545	< 0.001
Nashville warbler	0.366	0.002	< 0.000	0.425	0.293	0.006
Northern parula	0.084	0.200	0.153	0.030	0.224	0.011
Chestnut-sided warbler	0.379	0.002	0.130	0.046	0.635	< 0.001
Magnolia warbler	0.222	0.031	< 0.000	0.918	0.131	0.013
Black-throated blue warbler	0.410	< 0.001	0.198	0.012	0.576	< 0.001
Yellow-rumped warbler	0.261	0.016	< 0.000	0.944	0.452	< 0.001
Black-throated green warbler	0.348	0.003	0.193	0.013	0.450	< 0.001
Blackburnian warbler	0.282	0.011	0.270	0.002	0.439	< 0.001
Black-and-white warbler	0.256	0.018	0.038	0.228	0.205	0.040
American redstart	0.381	0.021	0.154	0.029	0.617	< 0.001
Ovenbird	< 0.000	0.770	0.131	0.046	0.633	< 0.001
Common yellowthroat	0.303	0.008	0.184	0.016	0.670	< 0.001
Canada warbler	0.133	0.110	0.182	0.017	0.635	< 0.001
Scarlet tanager	0.497	< 0.001	0.101	0.078	0.457	< 0.001
Rose-breasted grosbeak	0.362	0.002	0.113	0.063	0.284	0.005
White-throated sparrow	0.318	0.006	0.068	0.139	0.365	0.001
Dark-eyed junco	0.205	0.040	< 0.000	0.673	0.201	0.006
No. of best models	5		0.0		25	
No. fit at $P < 0.05$	19		10		30	
$\bar{A} - r^2$	0.23		0.09		0.40	

paper birch cover-types; the species is listed as a bird of deciduous forests in Bull and Farrand (1977) (p. 654). Red-eyed vireo (*Vireo olivacea*) is another species whose model associates it most strongly with paper birch and northern hardwood, and agrees with the deciduous forest listing in Bull and Farrand (1977) (p. 660). Models for red-breasted nuthatch (*Sitta carolinensis*), golden-crowned kinglet (*Regulus satrapa*), yellow-rumped warbler, magnolia warbler, blackburnian warbler (*Dendroica fusca*), black-and-white warbler, and dark-eyed junco contain only coniferous forest cover-types as the highest 2 cover types (Table 2). All are listed as birds of coniferous

forests in Bull and Farrand (1977) (pp. 685, 687, 691, 692, 704, 708).

Some cover-type models are problematic. Chestnut-sided warbler (*Dendroica pensylvanica*) and scarlet tanager (*Piranga olivacea*), for example, are listed as a deciduous forest species in Bull and Farrand (1977) (pp. 573, 655), but their cover-type models indicate that they are primarily associated with white pine and aspen cover-types and white pine and swamp hardwoods, respectively (Table 2). Some insight into these apparent contradictions is provided by stand structure, which shows that white pine stands of both size-classes contained consider-

Table 2
Expected log number of each species for each forest cover type^a, estimated from regressions with forest cover-type as a dummy variable, for the White Mountains, New Hampshire, and Maine, USA

	AS	PB	NH	SH	BF	WP	SF	EH
Least flycatcher	0.000	0.586	0.419	0.000	0.000	0.000	0.151	0.000
Red-breasted nuthatch	0.437	0.301	0.075	0.119	0.551	0.564	0.756	0.376
Winter wren	0.000	0.075	0.181	0.551	0.314	0.119	0.100	0.501
Golden-crown kinglet	0.000	0.075	0.075	0.000	0.444	0.270	0.569	0.309
Red-eyed vireo	0.978	1.134	1.001	0.990	0.389	0.688	0.519	0.926
Nashville warbler	0.890	0.339	0.377	0.001	0.514	0.701	0.699	0.620
Chestnut-sided warbler	0.639	0.000	0.200	0.075	0.000	0.711	0.000	0.288
Magnolia warbler	0.151	0.000	0.038	0.000	0.195	0.119	0.400	0.339
Black-throated blue warbler	0.437	0.931	0.448	0.573	0.075	0.050	0.519	0.129
Yellow-rumped warbler	0.150	0.194	0.075	0.000	0.495	0.669	0.410	0.808
Black-throated green warbler	0.386	0.751	0.592	0.586	0.120	0.120	0.080	0.738
Blackburnian warbler	0.119	0.544	0.307	0.539	0.800	0.570	0.813	0.611
Black-and-white warbler	0.195	0.151	0.480	0.413	0.595	0.734	0.180	0.357
American redstart	0.629	0.349	0.658	0.465	0.000	0.150	0.129	0.230
Common yellowthroat	0.423	0.000	0.157	0.075	0.000	0.595	0.151	0.317
Scarlet tanager	0.000	0.413	0.238	0.608	0.075	0.615	0.000	0.050
Rose-breasted grosbeak	0.707	0.615	0.443	0.194	0.194	0.269	0.209	0.362
White-throated sparrow	0.750	0.000	0.398	0.269	0.400	0.719	0.585	0.180
Dark-eyed junco	0.000	0.194	0.075	0.075	0.389	0.495	0.230	

^aAS = Aspen, PB = Paper birch, NH = Northern hardwoods, SH = Swamp hardwoods, BF = balsam fir, WP = White pine, SF = Spruce-fir, EH = Eastern hemlock.

able deciduous inclusions, especially in the 2–10 cm dbh size class (Table 4). Likewise, black-throated green- and black-throated blue warblers (*Denroica caerulescens*), listed as a birds of coniferous forests in Bull and Farrand (1977) (pp. 690, 700), have models that show deciduous and coniferous cover-types as important (Table 2). Black-throated green warbler is expected primarily in eastern hemlock according to the model, but it also is strongly associated with several deciduous types: paper birch, northern hardwoods, and swamp hardwoods. While eastern hemlock has considerable deciduous basal area in the stands sampled, paper birch has substantial softwood basal area in stems > 10 cm dbh in the poletimber size-class, as do northern hardwoods in sawtimber and large sawtimber, and sawtimber-sized swamp hardwoods (Table 4). Black-throated blue warbler, primarily associated with paper birch according to the cover-type model, also was strongly associated with white pine, which contained considerable deciduous basal area in stems > 10 cm dbh, especially in poletimber (Table 4).

In sum, cover-type is sometimes a good descriptor of species distributions, but not reliably so across species. Bird species models that look spurious are sometimes rendered understandable if the stand structure is known.

4.2. Size-class associations

Few published studies of eastern North American forest bird distributions by timber size-class exist. Field guides, e.g., Peterson (1980) list the general habitat types in which species are found, as does the Check-list of North American Birds (American Ornithologists' Union, 1983 and suppl.). Matrices of bird species occurrences by size-class within cover-type are provided by Green (1995) and DeGraaf and Rudis (1986); both compilations report syntheses and interpretations of the voluminous literature on the natural histories and habitat association of forest birds in eastern North America. Ten bird species showed significant ($P < 0.05$) size-class models (Table 3). As before, we used the magnitude of the expected values as a measure of importance of each size-class for each species. Of these, sapling stands were most important for 4 species, mature stands for 2 species, and large sawtimber stands for 3 species.

Table 3

Expected log number of each species for each stand size-class^a, estimated from regressions with size-class as a dummy variable, for the White Mountains, New Hampshire and Maine, USA

	S	Y	M	L
Eastern wood-pewee	0.100	0.123	0.321	0.539
Northern parula	0.166	0.086	0.145	0.469
Chestnut-sided warbler	0.593	0.164	0.183	0.076
Black-throated blue warbler	0.050	0.457	0.636	0.389
Black-throated green warbler	0.000	0.482	0.508	0.770
Blackburnian warbler	0.130	0.520	0.752	0.612
American redstart	0.700	0.229	0.314	0.574
Ovenbird	0.783	0.980	1.070	1.047
Common yellowthroat	0.512	0.119	0.167	0.151
Canada warbler	0.577	0.463	0.151	0.314

^aS = sapling, Y = poletimber, M = sawtimber, L = large sawtimber.

For one species, ovenbird, all size-classes from poletimber through large sawtimber were about equally important. For no species was poletimber alone important. Chestnut-sided warbler, American redstart (*Setophaga ruticilla*), common yellowthroat (*Geothlypis trichas*), and Canada warbler (*Wilsonia canadensis*) all showed strongest associations with sapling stands. Both chestnut-sided warbler and American redstart are widely known as birds of young (deciduous) forests (Green, 1995, pp. 139, 140; DeGraaf and Rappole, 1995, pp. 417, 445). The latter 2 species may occur in early-successional forests but also in deciduous understories within mature forests (DeGraaf and Rudis, 1986; DeGraaf and Rappole, 1995, pp. 459, 463; American Ornithologists' Union, 1983, pp. 628, 633).

The sawtimber stands that we sampled contained substantial understory components, and most sapling stands except aspen contained partial overstories of trees > 10 cm dbh, especially spruce–fir (Table 4). Thus, the distributions of bird species that were associated with either even-aged sapling stands or sawtimber stands with well-developed understories generally agree with reported habitat associations, but the forest understory species are not adequately described by size-class alone. Size-class associations for these species are best examined in light of the structure of the sampled stands.

Black-throated blue- and blackburnian warbler were most strongly associated with mature forest (Table 3); the former species nests in dense under-

Table 4
Structural characteristics of forest cover-types and size-classes surveyed for breeding birds in the White Mountains, New Hampshire, USA

Cover Type	Size-Class	Density (stems/ha) by dbh class (cm)				Basal area (m ² /ha)				Canopy Closure (%)	Ground cover (%)
		Trees		Stems	Snags	Coniferous stems		Deciduous stems			
		> 10	2–10	< 2	> 10	> 10 cm ^a	2–10 cm ^b	> 10 cm ^c	2–10 cm ^d		
Aspen	sapling	0	9107	38,871	0.0	0.0	0.0	0.0	7.1	85	40
	poletimber	1150	5402	3393	66.4	4.9	9.0	24.3	0.6	89	18
Aspen	poletimber	763	1473	2544	33.2	0.8	3.3	23.1	0.6	93	40
	sawtimber	808	491	893	66.4	3.1	0.0	28.3	1.8	91	32
N. hardwood	sapling	77	12,366	19,196	5.2	0.0	0.1	3.5	11.3	95	22
	poletimber	84	1518	5446	44.2	1.4	0.1	16.7	4.4	90	48
N. hardwood	sawtimber	791	714	1853	66.4	3.1	0.2	35.8	1.4	90	52
	lg. sawtimber	708	580	312	44.2	3.0	0.7	34.4	0.8	93	22
N. hardwood	poletimber	675	2098	12,991	33.2	1.3	0.3	15.2	2.5	90	42
	sawtimber	741	268	1384	177.0	7.3	0.1	24.9	0.4	91	60
Swamp hardwood	poletimber	1770	3750	312	0.0	25.9	6.7	7.5	2.4	83	22
	sawtimber	372	68	402	132.7	36.1	0.6	21.2	0.3	80	52
Balsam fir	poletimber	1217	1027	2232	110.6	35.2	2.4	8.3	0.7	87	15
	sawtimber	575	1071	2768	55.3	48.4	1.6	3.0	1.1	86	12
White pine	sapling	1681	3348	357	44.2	19.7	9.3	5.9	0.4	87	8
	poletimber	1217	402	44.2	44.2	31.9	0.3	7.0	1.3	84	25
White Pine	poletimber	1449	446	4196	33.2	20.7	0.7	22.2	0.6	85	32
	sawtimber	1394	893	223	66.4	35.1	2.8	24.3	0.4	87	18
E. hemlock	poletimber	730	268	848	33.2	28.7	0.7	6.4	0.1	87	30
	lg. sawtimber	697	45	2812	11.1	26.1	10.1	0.2	0.0	85	40

^aTotal coniferous basal area (m²)/ha of stems > 10 cm dbh.

^bTotal coniferous basal area (m²)/ha of stems 2–10 cm dbh.

^cTotal deciduous basal area (m²)/ha of stems > 10 cm dbh.

^dTotal deciduous basal area (m²)/ha of stems 2–10 cm dbh.

Table 5
Relationship of stand structure^a to log number of breeding birds for the White Mountains of New Hampshire and Maine, USA

Species	Intercept	ACLOS	GCV	LNLC	LNLD	LNMC	LNMD	LNST	LNNS	LVLC	LVLD	LVMC	LVMD	LVSC	LVSD	A-r ²	P
Yellow-bellied sapsucker ^b	–	+	+	–	–	–	–	–	+	+	+	+	+	–	–	0.228	0.022
Eastern wood-pewee ^b	–	+	–	–	–	–	–	–	+	+	+	–	+	+	+	0.556	<0.001
Least flycatcher ^b	–	+	–	–	–	–	–	–	+	+	+	–	+	+	+	0.720	<0.001
Blue jay	+	–	–	–	–	+	–	–	+	–	–	–	–	–	–	0.236	0.019
Black-capped chickadee	+	–	–	–	–	+	+	+	+	–	+	–	–	–	–	0.259	0.012
Red-breasted nuthatch	+	+	–	–	+	–	–	+	+	–	–	+	–	–	–	0.625	<0.001
Winter wren	+	–	+	+	–	–	–	–	–	–	+	–	–	+	–	0.401	0.001
Golden-crown kinglet	+	–	–	+	–	–	–	+	–	–	–	–	–	–	–	0.360	0.004
Veery ^b	–	+	+	+	–	–	+	+	–	–	–	+	–	–	–	0.261	0.041
Swainson's thrush ^b	+	–	–	+	–	–	+	+	–	–	–	–	–	–	–	0.362	0.002
Wood thrush ^b	+	–	–	–	–	–	+	+	+	+	+	–	–	+	+	0.294	0.026
Solitary vireo ^b	+	–	–	–	–	–	–	+	+	+	+	–	–	–	–	0.157	0.040
Red-eyed vireo ^b	–	–	–	–	–	–	–	–	+	+	+	–	+	–	–	0.545	<0.001
Nashville warbler ^b	+	–	–	–	–	–	+	+	–	–	–	–	–	–	–	0.293	0.006
Northern parula ^b	+	–	–	–	–	–	–	+	+	+	–	–	–	–	–	0.224	0.011
Chestnut-sided warbler ^b	+	–	–	+	+	–	–	+	+	–	–	–	+	–	–	0.635	<0.001
Magnolia warbler ^b	+	–	–	–	–	–	–	–	+	+	–	–	–	–	–	0.131	0.013
Black-throated blue warbler ^b	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	0.576	<0.001
Yellow-rumped warbler ^b	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–	0.452	<0.001
Black-throated green warbler ^b	–	+	+	–	–	–	–	–	–	+	+	–	–	+	+	0.450	<0.001
Blackburnian warbler ^b	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.439	<0.001
Black and white warbler ^b	–	+	–	+	+	–	–	–	–	–	–	–	+	–	–	0.205	0.40
American redstart ^b	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.617	<0.001
Ovenbird ^b	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.633	<0.001
Common yellowthroat ^b	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.670	<0.001
Canada warbler ^b	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.635	<0.001
Scarlet tanager ^b	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.457	<0.001
Rose-breasted grosbeak ^b	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	0.284	0.005
White-throated sparrow	+	–	–	+	+	–	–	–	–	–	–	–	–	–	–	0.365	0.001
Dark-eyed junco	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.201	0.006

Significance of individual model variables was denoted with + for $P < 0.10$, + for $P < 0.05$, or + for $P < 0.01$. Overall model adjusted r^2 ($A-r^2$) and probability of null model are also provided.

^aSee Table 4 for vegetation measurements.

^bNeotropical migrant.

stories of mature forests (DeGraaf and Rappole, 1995, p. 422), but was too uncommon in Lake States forests to be associated with size-class habitats (Green, 1995, p. 139). Blackburnian warbler was primarily associated with mature (conifer) habitat (Green, 1995, p. 140). From a size-class standpoint, these species are properly associated with mature forest.

Species associated with large-sawtimber stands included eastern wood-pewee (*Contopus virens*), northern parula, and black-throated green warbler (Table 3). Such a size-class is not reported as a distinct habitat for eastern forest birds, and is subsumed under mature forest. Each of the above species occurs in large-sawtimber stands, which contain at least half the stocking in trees > 51.0 cm dbh for softwoods and > 61 cm for hardwoods (DeGraaf and Rudis, 1986, p. 15). Large sawtimber and old-growth stands in New Hampshire tend to have widely-spaced large trees and well-developed understories, but also tend to have wide ranges in overstory and understory tree sizes and can be quite patchy in distribution. Hardwood large-sawtimber stands are found on fine till soils and enriched sites; softwood large-sawtimber stands are found on silty sediments and on wet compact tills (Leak, 1987). The above three species' habitat associations are different but all are commonly contained in large sawtimber stands: wood-pewee is common in open deciduous, coniferous, or mixed stands (American Ornithologists' Union, 1983, p. 449; DeGraaf and Rappole, 1995, p. 307), northern parula in stands with bearded lichen (*Usnea*) (Green, 1995, p. 138; Bent, 1953), and black-throated green warbler in open coniferous or mixed stands (American Ornithologists' Union, 1983, p. 613). Our large-sawtimber stands had relatively low densities of large trees and softwood components (Table 4); presence of lichen was not recorded. In sum, among species showing size-class affinities, interpretation of the relationships involves assessment of the structure of the associated stands.

4.3. Stand structure associations

Of the 31 species tested, within-stand structure explained a significant amount of variation in log numbers for 30 species. The number of significant

regression coefficients ($P < 0.10$) was used as a measure of the importance or ability of the variables to explain the variation in log numbers (Table 5).

Of the 14 stand structure variables used in the analyses, total foliage volume of large and mid-size deciduous trees were significant for 15 species each; density of mid-size deciduous trees, total woody stem density, and total deciduous understory volume were significant for 14 species each. Total foliage volume of large coniferous trees was significant for 13 species, and the density and foliage volume of mid-size conifers were significant for 12 species. Each of the other 6 variables were significant for 5–11 bird species (Table 5).

The most frequent significant predictors of relative abundance among the 24 Neotropical (long-distance) migratory species were the density of mid-size deciduous trees (13 species, 6 positive, 7 negative), foliage volume of mid-size deciduous trees (12 species; 5 positive, 7 negative), foliage volume of deciduous understory (12 species; 7 positive, 5 negative). Among the 6 resident/short-distance migrants, the most frequent significant predictors of relative abundance were woody stem density (4 species; 3 positive, 1 negative) and foliage volume of large trees (4 species; 2 positive, 2 negative). Although each species studied had a unique set of structural habitat affinities, multi-layered stands are apparently more important to long-distance migrants, in general, than to resident/short-distance migrants.

Canopy closure was a significant predictor of the relative abundances of comparatively few species: 6 Neotropical migrants (2 positive, 4 negative) and 3 resident/short distance migrants (all negative) (Table 5). In sum, for species that usually occur in poletimber and sawtimber stands, the vertical complexity of stands is more strongly associated with forest bird abundance than is canopy closure, especially for long-distance migratory species.

5. Discussion

This paper compares the relative abilities of forest cover-type, stand size-class, and stand structure to predict the relative abundances of breeding birds in New England forests. Stand structure was a better predictor of the relative abundances of breeding for-

est birds than either cover-type or size-class. Ours is the first attempt that we know of to compare these habitat measures, so comparison with similar studies is difficult. Lynch and Whigham (1984), in a study of 183 Maryland forests > 5 ha found that vegetation characteristics were more important predictors of the relative abundances of individual bird species than were patch area or patch isolation.

Robbins et al. (1989) in a study of 469 forest sites > 0.5 ha in Maryland and adjacent areas in Pennsylvania, Virginia and West Virginia found forest area to be the most important habitat correlate for 38 of 75 bird species. Patch size is an important variable to include in habitat measurements in the highly fragmented mid-Atlantic region, but is not relevant in extensively forested northern New England where our study was conducted. Robbins et al. (1989) surveyed birds in a variety of forest types in 4 physiographic regions ranging from high-elevation northern hardwoods and oak-hickory in the Allegheny Mountains to oak-pine and loblolly pine types on the lower eastern shore of Maryland and Virginia. It is likely that, if forest cover-type were an important predictor of bird occurrence, the relationships to forest area would have been confounded.

Stand size-class is (perhaps) a poor indicator of bird occurrence not only because it is based on overstory conditions and because it masks major differences in bird assemblages between hardwood and coniferous forests, but also because stands of given species, spacings, and sites (i.e., capacity to produce trees of a given size) develop in characteristic patterns (Oliver and Larson, 1990, p. 41). Crown shapes result from species' inherent growth forms and environmental conditions; depending on species, the terminal shoot more or less controls the length and orientation of lateral branches. Trees with strong apical control (many conifers, especially *Picea* and *Abies*) develop conical or columnar shapes, and in stands of such species the canopy closes at heights well below the tops of the trees. Trees with weak apical control (many hardwoods, especially *Fagus* and *Acer saccharum*) develop flat-topped crowns; canopy closure in stands dominated by such species occurs at or near the top of the canopy. Strong apical control creates a canopy with high 'relief' or 'topography'; weak apical control creates a relatively flat canopy upper surface. Also, softwood stands tend

toward much higher densities and basal areas than do hardwood stands. These structural differences between hardwoods and softwoods (or among hardwoods or among softwood stands depending on species) are obscured by size-class alone, and likely render size-class per se a poor predictor of bird species occurrence.

Foliage gleaning bird species show strong preferences for tree species upon which they forage for insect prey in New England forests (Holmes and Robinson, 1981). These preferred tree species may provide sites where food resources are more abundant and/or insect prey is more easily detectable or accessible. Size-class does not adequately capture this level of habitat detail nor does forest cover-type in many instances.

Studies in Europe (Oelke, 1966), England (Moore and Hooper, 1975), eastern North America (Bond, 1957), especially in the mid-Atlantic states (Linehan et al., 1967; Galli et al., 1976; Robbins, 1980; Whitcomb et al., 1981) have examined the effects of habitat fragmentation on forest birds; forest patch size is strongly related to both bird species composition and nesting success (see review by Askins et al., 1990). Robbins (1980) first analyzed the relative importance of vegetation aspects, forest isolation, and patch area on forest bird composition in 67 forest islands in the mid-Atlantic region; canopy height and forest isolation were the most consistently important predictors of the abundances of 51 bird species; patch area alone was significantly correlated with only 6 species' abundances, although, as noted by Lynch and Whigham (1984), patch area and vegetation characteristics were possibly intercorrelated. In their own large-scale study, Lynch and Whigham (1984) found that vegetation characteristics, rather than patch geometry, were the most important factors in determining bird community composition and local abundance of individual bird species.

Studies of the relationship between habitat heterogeneity and bird species diversity (MacArthur and MacArthur, 1961; MacArthur et al., 1962, 1966; Recher, 1969; Karr and Roth, 1971) and between forest habitat structure and bird species composition (Cody, 1974, 1978; James, 1971; Shugart and James, 1973; Anderson and Shugart, 1974; Whitmore, 1975, 1977; DeGraaf, 1992) have established a strong cor-

relation between habitat physiognomy and bird community composition for temperate forests in North America, Europe, and elsewhere. Furthermore, in an exhaustive study of habitat associations of forest birds at 8 study sites in eastern North America (Maryland, Ohio, Tennessee, Maine, Michigan, and Vermont), habitat preferences, although quite specific for each species, were shown to be remarkably consistent among widely different parts of species' ranges (Noon et al., 1980).

The spatial distribution of habitat patches is commonly estimated by remote sensing, from either aerial photographs or satellite imagery. The nature of vegetation character or structure can be assessed using aerial photography at various scales: the larger the scale, the more the structure can be detailed. For example, at scales of 1:25,000–1:100,000, broad vegetative types can be recognized, largely by inferential processes; at scales of 1:10,000–1:25,000, direct identification of major cover-types and species occurring in pure stands can be identified; at scales of 1:2500–1:10,000 individual trees and shrubs can be identified and their heights estimated (Avery and Berlin, 1985, p. 269). Classification and mapping of forest cover, especially using satellite imagery, is problematical. Boundaries between classification units generally constitute transition zones (Hengvelde, 1990) rather than sharp edges represented by polygon peripheries (Miller, 1996). Therefore, on most depictions of forested areas a somewhat continuous gradation among units is represented as a discrete boundary (Lowell, 1994). Furthermore, forest landcover classifications built upon satellite imagery usually do not include species composition or structural configuration of the forest (Miller, 1996).

Large-scale (landscape, regional) efforts to identify important habitats, assess degree of habitat protection from development, or monitor species/habitat trends are important to conservation; for forest bird species, such efforts must include estimates of the factors to which the species of concern are associated. In the case of New England forest birds, it appears that forest structure plays a more important role in predicting species' abundance than do stand size-class or cover-type. Given the consistency of bird species' habitat relationships, such is likely the case elsewhere in these species' ranges. Forest management that includes forest bird habitat en-

hancement should consider the details of stand structure and not rely solely upon cover-type composition or a distribution of timber size-classes to meet bird habitat needs. Such efforts will require inventory of key structural features (e.g., DeGraaf et al., 1992) and not rely on remote sensing to monitor forest conditions.

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Appendix A. Common and scientific names of birds observed in the White Mountains, New Hampshire and Maine, 1979–1980

Broad-winged hawk	<i>Buteo platypterus</i>
Ruffed grouse	<i>Bonasa umbellus</i>
American woodcock	<i>Scolopax minor</i>
Black-billed cuckoo	<i>Coccyzus erythrophthalmus</i>
Ruby-throated hummingbird	<i>Archilochus colubris</i>
Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>
Downy woodpecker	<i>Picoides pubescens</i>
Hairy woodpecker	<i>Picoides villosus</i>
Three-toed woodpecker	<i>Picoides tridactylus</i>
Black-backed woodpecker	<i>Picoides arcticus</i>
Northern flicker	<i>Colaptes auratus</i>
Pileated woodpecker	<i>Dryocopus pileatus</i>
Olive-sided flycatcher	<i>Contopus borealis</i>
Eastern wood-pewee	<i>Contopus virens</i>
Yellow-bellied flycatcher	<i>Empidonax flaviventris</i>
Alder flycatcher	<i>Empidonax alnorum</i>
Willow flycatcher	<i>Empidonax traillii</i>
Least flycatcher	<i>Empidonax minimus</i>
Eastern Phoebe	<i>Sayornis phoebe</i>
Great crested flycatcher	<i>Myiarchus crinitus</i>
Blue jay	<i>Cyanocitta cristata</i>

Appendix A (continued)

American crow	<i>Corvus brachyrhynchos</i>
Common raven	<i>Corvus corax</i>
Black-capped chickadee	<i>Parus atricapillus</i>
Boreal chickadee	<i>Parus hudsonicus</i>
Red-breasted nuthatch	<i>Sitta canadensis</i>
White-breasted nuthatch	<i>Sitta carolinensis</i>
Brown creeper	<i>Certhia americana</i>
Winter wren	<i>Troglodytes troglodytes</i>
Golden-crowned kinglet	<i>Regulus satrapa</i>
Ruby-crowned kinglet	<i>Regulus calendula</i>
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>
Veery	<i>Catharus fuscescens</i>
Swainson's thrush	<i>Catharus ustulatus</i>
Hermit thrush	<i>Catharus guttatus</i>
Wood thrush	<i>Hylocichla mustelina</i>
American robin	<i>Turdus migratorius</i>
Gray catbird	<i>Dumetella carolinensis</i>
Cedar waxwing	<i>Bombycilla cedrorum</i>
Solitary vireo	<i>Vireo solitarius</i>
Philadelphia vireo	<i>Vireo philadelphicus</i>
Red-eyed vireo	<i>Vireo olivaceus</i>
Golden-winged warbler	<i>Vermivora chrysoptera</i>
Tennessee warbler	<i>Vermivora peregrina</i>
Nashville warbler	<i>Vermivora ruficapilla</i>
Northern parula	<i>Parula americana</i>
Yellow warbler	<i>Dendroica petechia</i>
Chestnut-sided warbler	<i>Dendroica pensylvanica</i>
Magnolia warbler	<i>Dendroica magnolia</i>
Cape May warbler	<i>Dendroica tigrina</i>
Black-throated blue warbler	<i>Dendroica caerulescens</i>
Yellow-rumped warbler	<i>Dendroica coronata</i>
Black-throated green warbler	<i>Dendroica virens</i>
Blackburnian warbler	<i>Dendroica fusca</i>
Pine warbler	<i>Dendroica pinus</i>
Bay-breasted warbler	<i>Dendroica castanea</i>
Blackpoll warbler	<i>Dendroica striata</i>
Black-and-white warbler	<i>Mniotilta varia</i>
American redstart	<i>Setophaga ruticilla</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Northern waterthrush	<i>Seiurus noveboracensis</i>
Mourning warbler	<i>Oporornis philadelphia</i>
Common yellowthroat	<i>Geothlypis trichas</i>

Canada warbler	<i>Wilsonia canadensis</i>
Scarlet tanager	<i>Piranga olivacea</i>
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>
Indigo bunting	<i>Passerina cyanea</i>
Rufous-sided towhee	<i>Pipilo erythrophthalmus</i>
Swamp sparrow	<i>Melospiza georgiana</i>
White-throated sparrow	<i>Zonotrichia albicollis</i>
Dark-eyed junco	<i>Junco hyemalis</i>
Rusty blackbird	<i>Euphagus carolinus</i>
Brown-headed cowbird	<i>Molothrus ater</i>
Purple finch	<i>Carpodacus purpureus</i>
White-winged crossbill	<i>Loxia leucoptera</i>
American goldfinch	<i>Carduelis tristis</i>

References

- American Ornithologists' Union, 1983. Check-list of North American birds. 6th edn. American Ornithologists' Union, Lawrence, KS. 877 pp.
- Anderson, S.H., Shugart, H.H., 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. *Ecology* 55, 828–837.
- Apfelbaum, S., Haney, A., 1981. Bird populations before and after wildfire in a Great Lakes pine forest. *Condor* 83, 347–354.
- Askins, R.A., Lynch, J.F., Greenberg, R., 1990. Population declines in migratory birds in eastern North America. *Current Ornith.* 7, 1–57.
- Avery, T.E., Berlin, G.L., 1985. Fundamentals of remote sensing and airphoto interpretation. Macmillan, New York, 472 pp.
- Beals, E.W., 1960. Forest bird communities in the Apostle Islands of Wisconsin. *Wilson Bull.* 72, 156–181.
- Belcher, C.F., 1980. Logging railroads of the White Mountains. Appalachian Mountain Club, Boston, MA, 242 pp.
- Bent, A.C., 1953. Life histories of North American wood warblers: Part I. US National Museum Bull. 203. Smithsonian Institution, Washington, DC, 367 pp.
- Bond, R.R., 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. *Ecol. Monogr.* 27, 351–384.
- Brown, E.R. (Ed.), 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. US Dept. Agric., Forest Service, Pacific Northwest Region Pub. No. R6-F and WL-192: Part 2. Portland, OR, 302 pp.
- Bull, J., Farrand, J., Jr., 1977. The Audubon Society field guide to North American birds—eastern region. Alfred A. Knopf, New York, 775 pp.
- Cody, M.L., 1974. Competition and the structure of bird communities. *Monogr. Pop. Ecology*, Vol. 7, 1–318. Princeton Univ. Press, Princeton, NJ.
- Cody, M.L., 1975. Towards a theory of continental species diversity: Bird distributions over Mediterranean habitat gradients. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and evolution*

- of communities. Harvard Univ. Press, Cambridge, MA, pp. 214–251.
- Cody, M.L., 1978. Habitat selection and interspecific territoriality among the sylviid warblers of England and Sweden. *Ecol. Monogr.* 48, 351–386.
- Cody, M.L., 1985. An introduction to habitat selection in birds. In: Cody, M.L. (Ed.), *Habitat selection in birds*. Academic Press, Orlando, FL, pp. 3–56.
- DeGraaf, R.M., 1987. Managing northern hardwoods for breeding birds. In: Nyland, R.D. (Ed.), *Managing northern hardwoods*. Faculty of Forestry Misc. Pub. 13. State Univ. of New York, Syracuse, pp. 348–362.
- DeGraaf, R.M., 1992. Effects of even-aged management on forest birds at northern hardwood stand interfaces. *For. Ecol. Manage.* 46, 95–110.
- DeGraaf, R.M., Rappole, J.H., 1995. Neotropical migratory birds: Natural history, distribution, and population change. Cornell Univ. Press, Ithaca, NY, 676 pp.
- DeGraaf, R.M., Rudis, D.D., 1986. New England wildlife: Habitat, natural history, and distribution. Northeastern Forest Experiment Station, US Dept. Agric., Forest Service, General Tech. Rep. NE-108, Broomall, PA, 491 pp.
- DeGraaf, R.M., Yamasaki, M., Leak, W.B., Lanier, J.W., 1992. New England wildlife: Management of forested habitat. Northeastern Forest Experiment Station, US Dept. Agric., Forest Service, General Tech. Rep. NE-144, Radnor, PA, 271 pp.
- Eyre, F.H., 1980. Forest cover-types of the United States and Canada. Soc. Am. Foresters, Washington, DC, 148 pp.
- Galli, A.E., Leck, C.F., Forman, R.T.T., 1976. Avian distribution patterns within different sized forest islands. *Auk* 93 (1976), 356–365.
- Green, J.C., 1995. Birds and forests. A management and conservation guide. Minnesota Dept. Nat. Resour. St. Paul, MN, 182 pp.
- Helle, P., 1985. Habitat selection of breeding birds in relation to forest succession in northeastern Finland. *Ornis Fennica* 62, 113–123.
- Hengvælde, R., 1990. Dynamic biogeography. Cambridge Univ. Press, Cambridge, England.
- Hilden, O., 1965. Habitat selection in birds. *Ann. Zool. Fenn.* 2, 43–75.
- Holmes, R.T., 1990. The structure of a temperate deciduous forest bird community: Variability in time and space. In: Keast, A. (Ed.), *Biogeography and ecology of forest bird communities*. SPB Academic Publishing, The Hague, The Netherlands.
- Holmes, R.T., Robinson, S.K., 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia* 48, 31–35.
- Holmes, R.T., Sherry, T.W., 1988. Assessing population trends of New Hampshire forest birds: Local vs. regional patterns. *Auk* 105, 756–768.
- Holmes, R.T., Sherry, T.W., Sturges, F.W., 1986. Bird community dynamics in a temperate deciduous forest: Long-term trends at Hubbard Brook. *Ecol. Monogr.* 56, 201–220.
- James, F.C., 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83, 215–236.
- James, F.C., Wamer, N.O., 1982. Relationships between temperate forest bird communities and vegetation structure. *Ecology* 63, 159–171.
- Karr, J.R., Roth, R.R., 1971. Vegetation structure and avian diversity in several New World areas. *Am. Nat.* 105, 423–435.
- Lack, D., 1933. Habitat selection in birds. *J. Anim. Ecol.* 2, 239–262.
- Lack, D., 1971. *Ecological isolation in birds*. Blackwell, Oxford, UK, pp. 1–404.
- Leak, W.B., 1987. Characteristics of five climax stands in New Hampshire. US Dept. Ag., Forest Service, NEFES Research Note NE-336, 5 pp.
- Linehan, J.T., Jones, R.E., Longcore, J.R., 1967. Breeding bird populations in Delaware's urban woodlots. *Audubon Field Notes* 21, 641–646.
- Lowell, L., 1994. Initial studies in fuzzy surface-based representations of forests. In: Congalton, R.G. (Ed.), *International symposium on the spatial accuracy of natural resource data bases*. Am. Soc. Photogram. and Remote Sensing, Bethesda, MD, pp. 168–177.
- Lynch, J.F., Whigham, D.F., 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biol. Cons.* 28, 287–324.
- MacArthur, R.H., MacArthur, J., 1961. On bird species diversity. *Ecology* 42, 594–598.
- MacArthur, R.H., MacArthur, J.W., Preer, J., 1962. On bird species diversity: II. Prediction of bird census from habitat measurements. *Am. Nat.* 96, 167–174.
- MacArthur, R.H., Recher, H., Cody, M., 1966. On the relation between habitat selection and species diversity. *Am. Nat.* 100, 319–332.
- Mengel, R., 1964. Species formation in wood warblers. *Living Bird* 3, 9–43.
- Miller, R.I., 1996. Modern approaches to mapping forest diversity. In: DeGraaf, R.M., Miller, R.I. (Eds.), *Conservation of faunal diversity in forested landscapes*. Chapman & Hall, London, pp. 595–614.
- Moore, N.W., Hooper, M.D., 1975. On the number of bird species in British woods. *Biol. Conserv.* 8, 239–250.
- Morse, D.H., 1971. The foraging of warblers isolated on small islands. *Ecology* 52, 216–228.
- Morse, D.H., 1977. The occupation of small islands by passerine birds. *Condor* 79, 399–412.
- Morse, D.H., 1985. Habitat selection in North American parulid warblers. In: Cody, M.L. (Ed.), *Habitat selection in birds*. Academic Press, Orlando, FL, pp. 131–157.
- Noon, B.R., Dawson, D.K., Inkley, D.B., Robbins, C.S., Anderson, S.H., 1980. Consistency in habitat preference of forest bird species. *Trans. North Am. Wildl. Nat. Resour. Conf.* 45, 226–244.
- Oelke, N., 1966. Thirty-five years of breeding bird census work in Europe. *Audubon Field Notes* 20, 635–642.
- Oliver, C.D., Larson, B.C., 1990. *Forest stand dynamics*. McGraw-Hill, New York, 467 pp.
- Peterson, R.T., 1980. *A field guide to the birds of eastern and central North America*. Houghton Mifflin, Boston, 384 pp.

- Recher, H.F., 1969. Bird species diversity and habitat diversity in Australia and North America. *Am. Nat.* 103, 75–80.
- Robbins, C.S., 1980. Effects of forest fragmentation on breeding bird populations in the Piedmont of the mid-Atlantic region. *Atlantic Nat.* 33, 31–36.
- Robbins, C.S., Dawson, D.K., Dowell, B.A., 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic states. *Wildl. Monogr.* 103, 1–34.
- Roth, R.R., 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57, 773–782.
- SAS Institute, 1988. SAS User's Guide. Version 6.04. SAS Inst., Cary, N.C., 1028 pp.
- Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'erchia, F., Edwards, T.C., Ulliman, J., Wright, R.G., 1993. Gap analysis: A geographic approach to protection of biological diversity. *Wildl. Monogr.* 123, 41.
- Scott, J.M., Jennings, M., Wright, R.G., 1996. Landscape approaches to mapping biodiversity. *BioScience* 46, 77–78.
- Sherry, T.W., Holmes, R.T., 1985. Dispersion patterns and habitat responses of birds in northern hardwoods forests. In: Cody, M.L. (Ed.), *Habitat selection in birds*. Academic Press, Orlando, pp. 283–309.
- Short, H.L., Hestbeck, J.B., 1995. National biotic resource inventories and GAP analysis. *BioScience* 45, 535–539.
- Shugart, H.H., James, D., 1973. Ecological succession of breeding bird populations in northwestern Arkansas. *Auk* 90, 62–77.
- Shugart, H.H., Patten, B.C., 1972. Niche quantification and the concept of niche pattern. In: Patten, B.C. (Ed.), *Systems analysis and simulation in ecology: II*. Academic Press, New York, 607 pp.
- Smith, K.G., 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. *Ecology* 58, 810–819.
- Smith, K.G., 1982. Drought-induced changes in avian community structure along a montane sere. *Ecology* 63, 952–961.
- Svardson, G., 1949. Competition and habitat selection in birds. *Oikos* 1, 157–174.
- Thomas, J.W. (Ed.), 1979. *Wildlife habitats in managed forests: The Blue Mountains of Oregon and Washington*. Agric. Handbook 553, Washington, DC, US Dept. Agric., 512 pp.
- Titterton, R.W., Crawford, H.S., Burgason, B.N., 1979. Songbird responses to commercial clearcutting in Maine spruce-fir forests. *J. Wildl. Manage.* 43, 602–609.
- Verner, J., Boss, A.S. (Eds.), 1980. *California wildlife and their habitats: Western Sierra Nevada*. Pacific Southwest Forest and Range Experiment Station, US Dept. Agric., Forest Service, General Tech. Rep. PSW-37, Berkeley, CA, 439 pp.
- Webb, W.L., Behrend, D.F., Saisorn, B., 1977. Effect of logging on songbird populations in a northern hardwood forest. *Wildl. Monogr.* 55, 6–36.
- Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K., Bystrak, D., 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Burgess, R.L., Sharpe, B.M. (Eds.), *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, pp. 125–201.
- Whitmore, R.C., 1975. Habitat ordination of passerine birds of the Virgin River Valley, southwestern Utah. *Wilson Bull.* 87, 65–74.
- Whitmore, R.C., 1977. Habitat partitioning in a community of passerine birds. *Wilson Bull.* 89, 253–265.
- Willson, M.F., 1974. Avian community organization and habitat structure. *Ecology* 55, 1017–1029.