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HIERARCHICAL COMPARISONS OF BREEDING BIRDS IN OLD-GROWTH CONIFER-HARDWOOD FOREST ON THE APPALACHIAN PLATEAU

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ABSTRACT.—I compared relative abundances of breeding birds in old-growth forest (≥300 years old) to surrounding landscapes using data from the Breeding Bird Census (BBC) and Breeding Bird Atlas (BBA). Eleven study plots (148 ha total) were established in relict, presettlement hemlock-white pine-northern hardwood (*Tsuga canadensis-Pinus strobus*) forest on the northern Appalachian Plateau, Pennsylvania. Of 56 breeding species recorded in old-growth forest, 34% were either uncommon (≤25% of BBA blocks) or rare (≤10% of BBA blocks) in adjacent landscape units. A species accumulation curve indicated that about 40 species recurred in old-growth habitat. This avian community included species less likely to occur in oldgrowth, forest interior species showing a statistically neutral relationship to oldgrowth, and habitat specialists more likely to reside in oldgrowth than in the landscape at large. The last group included several taxa linked to structural features of oldgrowth elsewhere in North America: Hairy Woodpecker (*Picoides villosus*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia americana*), Winter Wren (*Troglodytes troglodytes*), Golden-crowned Kinglet (*Regulus satrapa*), *Empidonax* flycatchers, and several species of arboreal *Dendroica* warblers. *Received 14 July 1998, accepted 4 Nov. 1998.*

Old-growth forests possess unique ecological characteristics that can exert profound influence on some bird populations and communities (Hunter et al. 1995, Dellasala et al. 1996). Ecological importance of oldgrowth to birds is poorly known in much of North America, largely because late successional forest outside the Pacific Northwest now occurs only in relict patches (Davis 1996). Ideally, the role of old-growth forest in facilitating avian diversity could be best evaluated by comparing species occurrences within entire landscapes made up of many different habitats.

What is the best way to evaluate bird distributions and abundances over multiple spatial scales? Results of studies on species occurrences at any one scale may conflict with results at alternative scales (Conroy and Noon 1996). In avian ecology, this concern may find expression as a tradeoff among within-habitat (α), between-habitat (β), and landscape (γ) diversity (Whittaker 1977, Wiens 1989). For avian conservation, management actions at local scales must be weighed against their consequences at broader scales in order to optimize benefits of land use (Flather 1996). A hierarchical framework is the method usually recommended to address such scale dependency (Kotliar and Wiens 1990).

I used a landscape hierarchy to evaluate bird distribution and abundance in old-growth forest, once a widespread vegetation type in eastern North America. Local species' occurrences in old-growth conifer-hardwood forest were compared to occurrences in the surrounding landscape using data from the Breeding Bird Census and Breeding Bird Atlas. Three questions were posed: (1) can a metric be devised to compare bird species occurrences across different spatial scales, (2) does old-growth forest harbor birds determined independently to be uncommon or rare in larger landscape units, and (3) which individual species are more likely to occur in oldgrowth than in the landscape as a whole?

METHODS

Study area.—Bird communities in oldgrowth were studied within three permanent forest reserves in Pennsylvania: Cook Forest State Park, Heart's Content, and Tionesta Scenic and Research natural areas in the Allegheny National Forest (41° 20′–41° 42′ N, 78° 56′–79° 15′ W). Tract sizes of old-growth habitat varied from 1000 ha at Tionesta to 60 ha at Heart's Content; each of these reserves is embedded within much larger contiguous tracts of younger managed forest. Landscape fragmentation is greater in Cook Forest where developed and agricultural lands virtually surround this 3000 ha reserve (which includes some 200 ha of oldgrowth in three sites). All reserves are located on the northern Appalachian Plateau (212Ga: Allegheny High

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Plateau Subsection, Northern Unglaciated Allegheny Plateau Section; Keys et al. 1995), a region characterized by broad, flattened ridges (500–700 m) and dissected by deep, V-shaped valleys. Higher precipitation and greater cloud cover create a cooler, more humid climate compared to adjacent regions (Whitney 1990).

Each reserve possesses relict stands of true old-growth, stands with extreme ecological maturity (Leverett 1996). The forest consists of hemlock-white pine-northern hardwoods (Nichols 1935), a cover type that most closely resembles USDA Forest Service CISC (continuous inventory of stand condition) types 4 and 8, Society of American Foresters forest type code 22 (Eyre 1980), and International Classification of Ecological Communities I.B.8.N.b.150 (USDA 1997). Canopy dominants include eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*), black birch (*Betula lenta*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*; Whitney 1990).

Understories are generally sparse with little herbaceous ground cover. Canopy trees at each site are 300–530 years old (Hough and Forbes 1943; Abrams and Orwig 1996; Stahle 1996; C. Nowack, pers. comm.), and so are beyond the threshold (275 years) at which unique structure begins to develop in this community type (Tyrrell and Crow 1994). Typical of forest in presettlement condition, most stands have ecological attributes that are rare or absent in younger, managed forests (e.g., 57 metric tons of coarse woody debris ha^{-1}; >⅓ of stand basal area in trees >70 cm diameter at breast height; Haney, unpubl. data).

Since the late 1800s conifer-hardwood forest in the eastern U.S. has been fragmented into isolated blocks, markedly reduced in area, and converted into cover types dominated by younger, shade intolerant hardwoods. On the northern Appalachian Plateau, the old-growth hemlock-hardwood forest once covered 2.4 million ha (Bjorkblom and Larson 1977), but today it is reduced to no more than 20% of its presettlement extent (Whitney 1990, Abrams and Ruffner 1995).

Data collection.—I used the Breeding Bird Census (BBC; Hall 1964) to evaluate bird species occurrences within old-growth habitat. Breeding Bird Census methodology is used primarily to assess local population density by counting the number of breeding territories on a few ha. Five BBC plots (15–18 ha each) were located in Cook Forest, two (10–12 ha) in Heart's Content, and four (12 ha) in Tionesta. Individual plots within sites at each reserve ranged from 200 m to 2500 m apart. Breeding birds were counted during eight or more visits to each plot during May and June 1994 using standard protocols (Hall 1964, Lowe 1993). Each plot was visited on a different day, usually within a few minutes of sunrise. Two visits were made at dusk. Each visit lasted about two hours, which resulted in a census speed of about 9 min ha^{-1} and is comparable to speeds deemed appropriate for relatively open forests (Engstrom and James 1984).

On each visit, an observer walked slowly along a flagged census line through the plot, delineating all bird territories on grid maps. Birds were detected both visually and acoustically, but most detections were acoustic. The census line was configured to place the observer no more than 50 m from any part of the plot so as to reduce detection bias from acoustic attenuation (Schieck 1997). Numbers of territories were then calculated from grid maps using standard spot-mapping procedures (Hall 1964).

The Pennsylvania Breeding Bird Atlas project (1983–1989) was a grid-based survey using techniques developed originally in Britain and Ireland, with standards modified for the northeastern U.S. (Laughlin 1982). Atlas projects are used primarily for broad mapping of avian distributions and rely upon a network of volunteer field ornithologists to document breeding evidence at three levels of certainty ("possible," "probable," and "confirmed"). In Pennsylvania, the basic sampling units consisted of 7.5′ U.S. Geological Survey topographic maps divided into six equal-size blocks formed longitudinally by 3.75′ intervals and latitudinally by 2.5′ intervals (Brauning 1992). Atlas efforts were undertaken in both summer and winter within known "safe" dates for nesting activity of all species. Based on previous theoretical and empirical work, blocks were considered adequately covered if 75–80% of the expected species were found, 10–20 hours of survey effort were expended, or 70 or more species were recorded.

Community level analyses.—To test whether sampling effort was adequate for characterizing the total species complement (S_{max}) of the old-growth bird community, I conducted two analyses on the area curve of cumulative species richness (S). The shape of species accumulation curves depends on the order in which samples are added, a feature not modeled well with parametric methods (Bunge and Fitzpatrick 1993). I used non-parametric routines to randomize sample order (PISCES 1.2 software, Windows 95 version; Henderson and Seahy 1997). For greater resolution in constructing the species accumulation curve, I first subsampled the BBC data at a scale of 3 ha. From each and all of the 11 original study plots, I randomly selected and ordered 3 ha subplots and scored bird species occurrences and territorial densities using methods identical to those used in the original large plots.

Accurate estimation of S_{max} is possible only if the species accumulation curve is derived from a homogenous community (Henderson and Seahy 1997). I first compared the mean randomized curve (1000 iterations) with a curve expected if all individual birds recorded over all the samples were assigned randomly to individual samples (Colwell and Coddington 1994). If the expected curve (Coleman et al. 1982) rises more sharply from its origin, then heterogeneity is greater than can be explained by chance. Such a result could indicate that the samples were a combination of distinct bird communities or derived from different habitats (Flather 1996).

Asymptotic models of species accumulation curves are usually appropriate for homogenous communities

(Henderson and Seahy 1997). I calculated S_{max} using a non-parametric maximum likelihood estimater (Raaijmakers 1987) in which sampling is assumed to be complete when the asymptotic estimate is equal to or less than the observed. This procedure was applied incrementally to larger combinations of randomly shuffled 3 ha subplots (1000 iterations each) until the "stopping rule" indicated that sampling of the old-growth bird community was sufficient.

Species level analyses.—I used incidence (frequency in a set of samples; Wright 1991) as the metric to compare individual species' occurrences in oldgrowth to their occurrence in landscape units. Incidence in old-growth samples was calculated by dividing the number of plots containing each species by 11. For Pennsylvania and the northern Appalachian Plateau, I used the proportion of BBA blocks recording that species for each of the two landscape divisions. The atlas program covered a total of 4928 and 2027 BBA blocks state and province wide, respectively (Brauning 1992). Species recorded in less than 25% and 10% of BBA blocks in either landscape division were considered uncommon and rare, respectively.

I compared incidence in oldgrowth (I_{OG}) to incidence statewide (I_{ST}) and province-wide (I_{AP}) with the normal deviate, *Z*, where:

$$Z = (I_1 - I_2)/(I \times (1 - I)(1/N_1 + 1/N_2))^{0.5},$$

and I and 1 − I are the joint probabilities of the combined incidences in the two sample proportions of finding and not finding that species, respectively (Snedecor and Cochran 1980). I used Pearson's product moment correlation to test whether incidence was related to the natural log of population density (number of breeding territories). Log transformations on population density were used to smooth variances in data composed of whole integers (Snedecor and Cochran 1980). Values of test statistics were considered significant at $P \leq 0.05$ unless otherwise indicated.

RESULTS

Community composition.—Fifty-six species were recorded in 148 ha of old-growth forest across the 11 study plots (Table 1). Thirteen species were found in only one plot (incidence value = 0.091). Another species, Downy Woodpecker (*Picoides pubescens*), was recorded in two plots, but less than one full territory was recorded in each plot. Without considering these 14 species, a recurring complement of 42 species was identified in which full breeding territories were established in two or more of the 11 study plots (Table 2).

The observed species accumulation curve (Fig. 1) did not differ from the curve expected in a homogenous community ($\chi^2 = 0.25$, $P > 0.05$, df = 27). Thus, this analysis gave no indication that more than one bird community was being sampled. The estimated asymptotic value (38.6) for species richness fell below the observed value (39) after 1000 randomizations of 28 3-ha subplots. This level of effort corresponded to 84 ha (57%) of the total area actually sampled in this study.

Species groups.—About one-third of all species recorded as breeders in old-growth conifer-hardwood were either uncommon or rare over broad spatial scales (Table 1). Nineteen species (34%) were more likely to occur in oldgrowth than in the landscape unit consisting of the entire state. Sixteen species (29%) were more likely to occur in oldgrowth than in the landscape unit of the northern Appalachian Plateau. Fifteen individual species were more likely to occur in oldgrowth than in the landscape at both state and province levels (Table 2). Red-shouldered Hawk (*Buteo lineatus*) and Barred Owl (*Strix varia*) were more likely to occur in oldgrowth than in the landscape unit consisting of the entire state but not the northern Appalachian Plateau.

Seventeen species were less likely to occur in old-growth forest than in the landscape at large (Table 2). This group included permanent resident, habitat generalists [e.g., American Crow (*Corvus brachyrhynchos*)] as well as some Neotropical migrants with more specific habitat preferences [e.g., cavity-nesting Great Crested Flycatcher (*Myiarchus crinitus*)].

No species showing negative association with oldgrowth (Table 2) was rare at the state level, and none of the species in this group was either rare or uncommon at the level of the physiographic province (Table 1). Only one species, Black-throated Blue Warbler (*Dendroica caerulescens*), was uncommon at the state level (15% of BBA blocks). Most species negatively associated with oldgrowth were very widespread within broad landscape units, occurring in 50–90% of the BBA blocks.

Based on statistical criteria, 10 species were neither more nor less likely to occur in oldgrowth than in at least one of the larger landscape units (Tables 1 and 2). All species in this group rely upon forest interior habitat, including the raptors Red-shouldered Hawk and Barred Owl, and Neotropical migrant songbirds such as Red-eyed Vireo (*Vireo oliva-*

TABLE 1. Relative occurrence of breeding birds in old-growth hemlock-white pine-hardwood forest on the northern Appalachian Plateau, Pennsylvania. Incidence (I) of each species in oldgrowth (proportion of study plots, $n = 11$) is compared to incidence across the entire state and within the physiographic province [proportion of Breeding Birds Atlas (BBA) plots recording the species; $n = 4928$ and 2027 blocks, respectively].

	Incidence			Comparison			
				$(I_{OG}) - (I_{ST})$		$(I_{OG}) - (I_{AP})$	
Species	Oldgrowth (I_{OG})	Statewide (I_{ST})	Appalachian Plateau (I_{AP})	Z^a	P	Z^a	P
Common Merganser (*Mergus merganser*)	0.091	0.046	0.087	0.71	>0.05	0.56	>0.05
Sharp-shinned Hawk (*Accipiter striatus*)	0.091	0.213	0.200	−0.99	>0.05	−0.90	>0.05
Red-shouldered Hawk (*Buteo lineatus*)	0.364	0.152	0.223	1.95	0.026	1.12	>0.05
Mourning Dove (*Zenaida macroura*)	0.273	0.917	0.835	−7.68	<0.001	−4.97	<0.001
Barred Owl (*Strix varia*)	0.455	0.218	0.277	1.90	0.029	1.31	>0.05
Ruby-throated Hummingbird (*Archilochus colubris*)	0.273	0.714	0.704	−3.23	0.001	−3.12	0.001
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.273	0.149	0.319	1.15	>0.05	−0.33	>0.05
Downy Woodpecker (*Picoides pubescens*)	0.182	0.890	0.855	−7.45	<0.001	−6.26	<0.001
Hairy Woodpecker (*Picoides villosus*)	0.909	0.632	0.643	1.90	0.029	1.84	0.033
Northern Flicker (*Colaptes auratus*)	0.091	0.917	0.873	−9.82	<0.001	−7.66	<0.001
Pileated Woodpecker (*Dryocopus pileatus*)	0.545	0.538	0.566	0.05	>0.05	−0.14	>0.05
Eastern Wood-Pewee (*Contopus virens*)	0.091	0.883	0.868	−8.11	<0.001	−7.49	<0.001
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	0.091	0.003	0.006	5.16	<0.001	3.51	<0.001
Acadian Flycatcher (*Empidonax virescens*)	0.818	0.358	0.234	3.18	0.001	4.54	<0.001
Least Flycatcher (*Empidonax minimus*)	0.182	0.369	0.636	−1.29	>0.05	−3.12	0.001
Greater Crested Flycatcher (*Myiarchus crinitus*)	0.182	0.709	0.640	−3.84	<0.001	−3.15	0.001
Blue Jay (*Cyanocitta cristata*)	0.636	0.954	0.939	−4.99	<0.001	−4.13	<0.001
American Crow (*Corvus brachyrhynchos*)	0.182	0.978	0.964	−17.31	<0.001	−13.17	<0.001
Common Raven (*Corvus corax*)	0.182	0.172	0.294	0.09	>0.05	−0.81	>0.05
Tufted Titmouse (*Baeolophus bicolor*)	0.273	0.809	0.641	−4.51	<0.001	−2.54	0.006
Black-capped Chickadee (*Poecile atricapillus*)	1.000	0.842	0.970	1.44	>0.05	0.58	>0.05
Red-breasted Nuthatch (*Sitta canadensis*)	0.727	0.041	0.064	11.27	<0.001	8.74	<0.001
White-breasted Nuthatch (*Sitta carolinensis*)	0.545	0.828	0.840	−2.48	0.006	−2.65	0.004
Brown Creeper (*Certhia americana*)	1.000	0.231	0.324	6.03	<0.001	4.76	<0.001
Winter Wren (*Troglodytes troglodytes*)	0.909	0.077	0.147	10.23	<0.001	7.04	<0.001
Golden-crowned Kinglet (*Regulus satrapa*)	0.182	0.037	0.057	2.53	0.006	1.77	0.038
Swainson's Thrush (*Catharus ustulatus*)	0.636	0.009	0.019	20.49	<0.001	13.82	<0.001
Hermit Thrush (*Catharus guttatus*)	1.000	0.278	0.492	5.33	<0.001	3.36	<0.001
Wood Thrush (*Hylocichla mustelina*)	0.182	0.912	0.892	−8.47	<0.001	−7.45	<0.001
American Robin (*Turdus migratorius*)	0.364	0.991	0.987	−20.49	<0.001	−16.25	<0.001
Cedar Waxwing (*Bombycilla cedrorum*)	0.182	0.824	0.919	−5.57	<0.001	−8.74	<0.001
Blue-headed Vireo (*Vireo solitarius*)	1.000	0.299	0.484	5.07	<0.001	3.41	<0.001

TABLE 1. CONTINUED

Species	Incidence			Comparison			
				$(I_{OG}) - (I_{ST})$		$(I_{OG}) - (I_{AP})$	
	Oldgrowth (I_{OG})	Statewide (I_{ST})	Appalachian Plateau (I_{AP})	Z[a]	P	Z[a]	P
Red-eyed Vireo (*Vireo olivaceus*)	1.000	0.931	0.959	0.90	>0.05	0.69	>0.05
Northern Parula (*Parula americana*)	0.091	0.101	0.099	−0.11	>0.05	−0.09	>0.05
Chestnut-sided Warbler (*Dendroica pensylvanica*)	0.091	0.407	0.686	−2.13	0.017	−4.23	<0.001
Magnolia Warbler (*Dendroica magnolia*)	1.000	0.151	0.315	7.82	<0.001	4.86	<0.001
Black-throated Blue Warbler (*Dendroica caerulescens*)	0.455	0.150	0.272	2.82	0.002	1.36	>0.05
Yellow-rumped Warbler (*Dendroica coronata*)	0.091	0.064	0.126	0.36	>0.05	−0.35	>0.05
Black-throated Green Warbler (*Dendroica virens*)	1.000	0.366	0.587	4.36	<0.001	2.78	0.003
Blackburnian Warbler (*Dendroica fusca*)	1.000	0.186	0.350	6.90	<0.001	4.50	<0.001
Bay-breasted Warbler (*Dendroica castanea*)[b]	0.091	—	—	—	—	—	—
Pine Warbler (*Dendroica pinus*)	0.364	0.060	0.057	4.21	<0.001	4.32	<0.001
Black-and-white Warbler (*Mniotilta varia*)	0.091	0.428	0.501	−2.26	0.012	−2.71	0.003
American Redstart (*Setophaga ruticilla*)	0.182	0.607	0.796	−2.88	0.002	−5.01	<0.001
Ovenbird (*Seiurus aurocapillus*)	0.364	0.746	0.827	−2.91	0.002	−4.03	<0.001
Mourning Warbler (*Oporornis philadelphia*)	0.091	0.048	0.111	0.66	>0.05	−0.21	>0.05
Common Yellowthroat (*Geothlypis trichas*)	0.182	0.960	0.975	−12.89	<0.001	−15.56	<0.001
Hooded Warbler (*Wilsonia citrina*)	0.364	0.288	0.313	0.55	>0.05	0.36	>0.05
Scarlet Tanager (*Piranga olivacea*)	1.000	0.868	0.903	1.29	>0.05	1.09	>0.05
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	0.364	0.639	0.835	−1.90	0.029	−4.17	<0.001
Indigo Bunting (*Passerina cyanea*)	0.091	0.946	0.931	−12.33	<0.001	−10.65	<0.001
Chipping Sparrow (*Spizella passerina*)	0.909	0.971	0.976	−1.22	>0.05	−1.44	>0.05
Dark-eyed Junco (*Junco hyemalis*)	1.000	0.271	0.528	5.42	<0.001	3.13	0.001
Brown-headed Cowbird (*Molothrus ater*)	0.364	0.877	0.834	−5.16	<0.001	−4.16	<0.001
Purple Finch (*Carpodacus purpureus*)	0.909	0.294	0.485	4.47	<0.001	2.81	0.003
American Goldfinch (*Carduelis tristis*)	0.091	0.944	0.924	−12.10	<0.001	−10.13	<0.001

[a] Test statistic (normal deviate) on the difference between proportions: positive values of Z indicate a greater incidence of that species in oldgrowth, negative values indicate lower incidence in oldgrowth.
[b] Unrecorded during the state's 5 year BBA project. From 1993–1995, an irruption of the elm spanworm *Ennomus subsignarius* affected much of Pennsylvania's forests. Several birds influenced by geometrid outbreaks were recorded during these breeding seasons for the first time: Bay-breasted Warbler, Blackpoll Warbler (*Dendroica striata*) and Evening Grosbeck (*Coccothraustes vespertinus*).

TABLE 2. Number of territories and population densities (number territories/10 ha) of the core community of breeding birds in all plots ($n = 11$) of old-growth hemlock-white pine-hardwood forest on the northern Appalachian Plateau, Pennsylvania.

Association: Species[a]	Total territories	Territorial density	
		Mean	SE
Positive old-growth affinity:			
Hairy Woodpecker (*Picoides villosus*)	12.5	0.50	0.42
Acadian Flycatcher (*Empidonax virescens*)	24.5	1.27	1.57
Red-breasted Nuthatch (*Sitta canadensis*)	10	0.40	0.36
Brown Creeper (*Certhia americana*)	31	1.58	0.71
Winter Wren (*Troglodytes troglodytes*)	30.5	1.73	0.98
Golden-crowned Kinglet (*Regulus satrapa*)	4	0.10	0.23
Swainson's Thrush (*Catharus ustulatus*)	35	2.08	2.42
Hermit Thrush (*Catharus guttatus*)	36.5	1.90	1.49
Blue-headed Vireo (*Vireo solitarius*)	88	4.57	2.26
Magnolia Warbler (*Dendroica magnolia*)	185	11.10	2.70
Black-throated Green Warbler (*Dendroica virens*)	176	9.41	5.36
Blackburnian Warbler (*Dendroica fusca*)	410	23.94	8.25
Pine Warbler (*Dendroica pinus*)	5	0.17	0.25
Dark-eyed Junco (*Junco hyemalis*)	83	4.09	0.92
Purple Finch (*Carpodacus purpureus*)	17	0.72	0.52
Neutral oldgrowth affinity:			
Red-shouldered Hawk (*Buteo lineatus*)[b]	2.5	0.09	0.13
Barred Owl (*Strix varia*)[b]	4.5	0.18	0.24
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	4	0.14	0.26
Pileated Woodpecker (*Dryocopus pileatus*)	5.5	0.25	0.31
Common Raven (*Corvus corax*)	1.5	0.07	0.19
Black-capped Chickadee (*Poecile atricapillus*)	24	1.14	0.62
Red-eyed Vireo (*Vireo olivaceus*)	110	5.22	3.06
Hooded Warbler (*Wilsonia citrina*)	15	0.87	1.40
Scarlet Tanager (*Piranga olivacea*)	42.5	2.23	1.08
Chipping Sparrow (*Spizella passerina*)	20	1.00	0.63
Negative old-growth affinity:			
Mourning Dove (*Zenaida macroura*)	3	0.09	0.21
Ruby-throated Hummingbird (*Archilochus colubris*)	2	0.06	0.11
Least Flycatcher (*Empidonax minimus*)	3.5	0.18	0.53
Great Crested Flycatcher (*Myiarchus crinitus*)	1.5	0.08	0.18
Blue Jay (*Cyanocitta cristata*)	10.5	0.45	0.35
American Crow (*Corvus brachyrhynchos*)	1.5	0.06	0.14
Tufted Titmouse (*Baeolophus bicolor*)	2	0.11	0.19
White-breasted Nuthatch (*Sitta carolinensis*)	7.5	0.27	0.31
Wood Thrush (*Hylocichla mustelina*)	1.5	0.09	0.25
American Robin (*Turdus migratorius*)	4.5	0.20	0.40
Cedar Waxwing (*Bombycilla cedrorum*)	2	0.10	0.23
Black-throated Blue Warbler (*Dendroica caerulescens*)	18	1.08	1.46
American Redstart (*Setophaga ruticilla*)	7.5	0.43	1.28
Ovenbird (*Seiurus aurocapillus*)	8	0.46	0.95
Common Yellowthroat (*Geothlypis trichas*)	2	0.06	0.14
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	5	0.24	0.44
Brown-headed Cowbird (*Molothrus ater*)	9	0.32	0.58

[a] Does not include species found only in one plot or for which less than one full territory was recorded (Table 1).
[b] Positively associated with oldgrowth at landscape level of entire state but not at level of physiographic province.

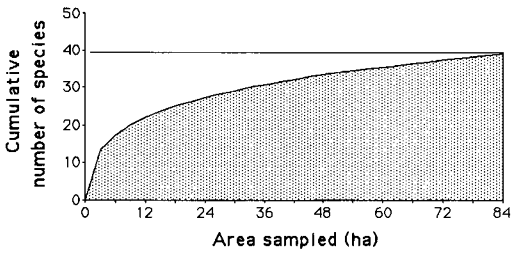

FIG. 1. Mean randomized accumulation curve (1000 iterations) of species richness in the bird community of old-growth conifer-hardwood forest on the northern Appalachian Plateau, Pennsylvania. Horizontal line indicates the putative asymptote of species richness as a function of area sampled. The asymptote was identified with a maximum likelihood estimater.

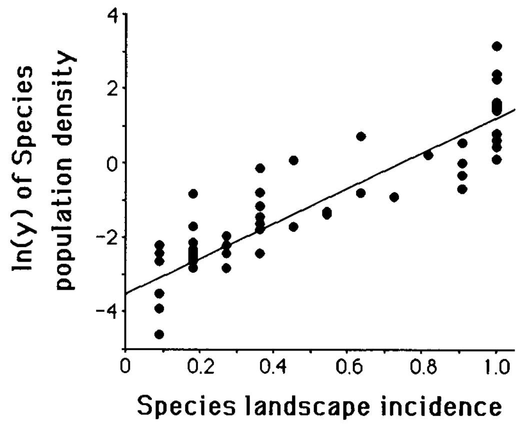

FIG. 2. Relationship between natural log of population density (number of breeding territories) and landscape incidence of all bird species (n = 56) found in old-growth conifer-hardwood forest of the northern Appalachian Plateau, Pennsylvania. Landscape incidence is based on the proportion of old-growth study plots (n = 11; Table 1) in which the species was recorded. Log of population density (y) is related to landscape incidence (x) by: $y = 4.741x - 3.513$, (r^2 = 0.805, $P < 0.001$).

ceus), Hooded Warbler (*Wilsonia citrina*), and Scarlet Tanager (*Piranga olivacea*).

Incidence versus population density.—Bird species that were rare or uncommon at landscape levels typically had low population densities locally as well. Incidence explained slightly more than 80% of the variation in the natural log of population size as assessed by territorial density (Fig. 2).

DISCUSSION

Old-growth affinities.—At both province and state levels, more than one-third of bird species were more likely to occur in old-growth conifer-hardwood forest than in the broader landscape. These species included some of Pennsylvania's rarest breeding birds. Yellow-bellied Flycatcher (*Empidonax flaviventris*) and Swainson's Thrush (*Catharus ustulatus*) are listed in the state as threatened and candidate-rare, respectively (D. A. Gross, pers. comm.). Pending investigation of specific habitat preferences for individual species, the 15 birds in this group (Table 2) are best regarded as old-growth associates rather than old-growth obligates. Nevertheless, it is notable that these species have diverse habitat affinities, including conifer [e.g., Red-breasted Nuthatch (*Sitta canadensis*)], hardwood [e.g., Blue-headed Vireo (*Vireo solitarius*)], and mixed forest cover types [e.g., Hairy Woodpecker (*Picoides villosus*)].

Several taxa identified as old-growth associates in this study have been linked repeatedly to late successional forest elsewhere throughout North America. Hairy Woodpeckers rely on mature forests with large snags and logs (Anthony et al. 1996, Shackelford and Conner 1998). Across broad geographic domains, Red-breasted Nuthatch, Brown Creeper (*Certhia americana*), Winter Wren (*Troglodytes troglodytes*), and Golden-crowned Kinglet (*Regulus satrapa*) form a recurring group that exploits coniferous cover and complex structure typical of older natural forests (DeGraaf et al. 1992, Hansen et al. 1995, Schieck et al. 1995, Anthony et al. 1996, Dellasala et al. 1996).

In other cases, regional counterparts of genera exhibited a common tendency to prefer mature forest. Acadian Flycatcher (*Empidonax virescens*) showed a greater likelihood of occurring in mesic old-growth forest relative to adjacent landscapes (Table 1), similar to Hammond's (*E. hammondii*) and Pacific-slope (*E. difficilis*) flycatchers in Oregon and British Columbia (Hansen et al. 1995, Schieck et al. 1995). Like their western congeners Hermit (*Dendroica occidentalis*) and Townsend's warblers (*D. townsendi*; Hansen et al. 1995, Schieck et al. 1995), several species of arboreal *Dendroica* warblers were far more likely to occur in old-growth hemlock-white pine-northern hardwood forest than in adjacent landscape units (Tables 1 and 2). Populations of Blackburnian Warblers (*D. fusca*) achieve particularly high densities in the oldest conifer-hardwood forests of this region (Haney and Schaadt 1996: fig. 6.1).

Two species, Red-shouldered Hawk and Barred Owl, were more likely to occur in oldgrowth than across the state as a whole (Table 1). Red-shouldered Hawks depend on mature forests with large trees for nest sites (Titus and Mosher 1981, Moorman and Chapman 1996). Barred Owls exhibit greater territorial occupancy and breeding propensity in this region's old-growth forest (Haney 1997).

Despite directional biases in comparisons of incidence across spatial scales (see *Sampling adequacy*), negative associations of bird species with oldgrowth may have had biological causes. Mourning Dove (*Zenaida macroura*), Blue Jay (*Cyanocitta cristata*), American Crow, and Brown-headed Cowbird (*Molothrus ater*; Table 2) all typically exploit landscapes with extensive anthropogenic disturbance (Martin 1988, Hoover and Brittingham 1993, Seitz and Zegers 1993, Rodenhouse et al. 1995). Consequently, they would be less expected to occur in mature tracts of reserved forest. Least Flycatcher (*Empidonax minimus*), Black-throated Blue Warbler, American Redstart (*Setophaga ruticilla*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*) more commonly exploit the deciduous habitats (Sherry and Holmes 1988, Steele 1993, Yahner 1993) typical of younger, regenerating forest now prevalent in this region (Alerich 1993). Ovenbirds (*Seiurus aurocapillus*) were probably scarce because of their preference for heavy ground cover (Burke and Nol 1998), a microhabitat virtually absent in the old-growth forest studied here.

Sampling adequacy.—Deletion of peripheral species and analysis of the asymptote on the species accumulation curve gave similar values for total species: 42 and 39 species, respectively. I conclude that census effort was adequate for characterizing the avian community in old-growth hemlock-white pine-northern hardwood forest on Pennsylvania's northern Appalachian Plateau. Numerical analyses indicated that the community sampled was in fact homogenous and an asymptotic limit to species richness (S_{max}) was achieved with little more than half the sampling effort actually undertaken (Fig. 1). Support for sampling adequacy is reassuring because limited amounts and local distributions of eastern old-growth forest often preclude obtaining larger sample sizes and greater sample dispersion in this scarce habitat type.

Use of bird species richness (S or S_{max}) to evaluate avian habitat can be problematic unless studies account for: (1) "core" members of the avifauna, (2) quantity and quality of sampling effort, (3) number of habitat types within areas, and (4) proximity of other habitats (Remsen 1994, Elphick 1997). The BBC method itself purposefully discounts non-territory holders, thereby eliminating nonbreeding species. I also established study plots within interiors of old-growth forest so as to avoid inflating or confounding species richness caused by proximity of different habitat patch types (Flather 1996).

Although BBC and BBA methods have distinct purposes and can have different quantities and qualities of observer effort, several factors facilitated comparisons of data from the two techniques in this study. First, species occurrence data from both methods were comparable by developing a common incidence metric. Second, both methods rely to some extent upon a measure of saturation in the cumulative number of species recorded in order to guage whether sampling is adequate. Third, both methods had similar levels of observer effort as measured by survey duration. All BBCs took 16.7–20.1 h to complete versus an average of 17 field-h per atlas block (Brauning 1992).

The BBC method's reliance on three or more records to score territorial occupancy, however, is more restrictive in tallying species occurrences than the BBA method. The latter includes "possible," "probable," and "confirmed" categories of breeders, and is therefore likely to include more species per unit effort. Greater numbers of species may also be detected with the BBA method because of the substantially larger areas covered (potentially hundreds or thousands of ha per block versus the tens of ha in most BBCs).

As a consequence of differences in the scope of effort between BBC and BBA methods, comparisons of incidence values (I) for individual species (Table 1) may be biased against detecting greater occurrence (and towards detecting lower occurrence) in old-growth habitat than in the landscape at large. Findings of positive old-growth association by individual species (Table 2) are more robust as a result. Negative and neutral associations with oldgrowth should be interpreted cautiously because more liberal listing of species under BBA methodology could elevate relative incidence values at state and province levels, thereby leading to false conclusions that no differences in species occurrences existed across spatial scales (Type II error).

Hierarchical comparisons.—Although scale is viewed as essential for interpreting distributional data in birds (Lacy and Bock 1986), logistical constraints and methodological inconsistencies often prevent hierarchical or multi-tiered approaches. Comparing local density of bird populations to density in a region as large as an entire state is impossible because the BBC method requires large investments in time for limited spatial coverage. Proportions are easy to derive from virtually any kind of sample, however, and a metric based on incidence enabled direct comparison of species occurrences in BBC plots and atlas blocks (Table 1).

Comprehensive coverage in Pennsylvania's atlas program also enabled more reliable comparisons of birds in oldgrowth to the wider landscape: all blocks, including those on the state's borders, were censused (Brauning 1992). Synoptic coverage allows evaluation of the likely impacts of potential actions on groups of bird species within a wider context. It would be easy to scale down from the eco-physiographic province or state levels used in this study to some smaller region of interest (e.g., county, national forest, watershed). Alternatively, BBA data from adjacent states could be aggregated to examine individual species occurrences across even larger landscape units. This spatial flexibility should enable better evaluation of potential consequences of local management prescriptions on the regional distributions of birds.

I used an incidence metric as a reasonable proxy for population size (Fig. 2). Several researchers have documented a general relationship between abundance and range size in birds (Bock and Ricklefs 1983, Lacy and Bock 1986, Mauer and Heywood 1993). This relationship may not indicate the existence of a particular ecological hypothesis (Wright 1991). Nevertheless, the generality that species with sparse distributions also have low population densities was confirmed in this study by documenting regional scarcity in several bird species that use a rare and very local habitat type.

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