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STRUCTURE, SEASONAL DYNAMICS, AND HABITAT RELATIONSHIPS OF AVIAN COMMUNITIES IN SMALL EVEN-AGED FOREST STANDS

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ABSTRACT.—Structure, stability, and habitat relationships of avian communities associated with small even-aged stands were studied for three consecutive winters and breeding seasons in aspen (*Populus* spp.) and mixed-oak (*Quercus* spp.) cover type in an area managed for Ruffed Grouse (*Bonasa umbellus*) habitat. Thirteen and 69 species were noted in six habitat types during winter and the breeding season, respectively. Trunk-bark foragers predominated in winter, particularly in uncut habitats; in contrast, the ground-shrub foraging guild predominated in the breeding season, especially in clearcut habitats. The six habitat types were segreated in two groups (uncut and clearcut) on the basis of the stability of the trunk-bark and ground-shrub foraging guilds in winter and the breeding season, respectively. Black-capped Chickadees (*Parus atricapillus*) in winter and Rufous-sided Towhees (*Pipilo erythrophthalmus*) in the breeding season were the most abundant species. Habitat variables describing overstory trees and snags were among those important to trunk-bark and sallier-canopy foraging guilds; variables describing shrub and understory vegetation were associated with the ground-shrub foraging guild. The habitat fragmentation created by the current cutting cycle has had no discernible negative impact on the avifauna, and species adapted to early-successional habitats have benefited. *Received 19 Apr. 1985, accepted 15 Aug. 1985.*

Habitat size and age are two major determinants of avian community structure in even-aged forest stands affected by clearcutting (e.g., Conner et al. 1979, Titterington et al. 1979, Crawford et al. 1981, Niemi and Hanowski 1984). If size of even-aged forest stands were held constant, but age were allowed to vary, then researchers could obtain better insight into the effects of vegetative complexity, which often is a function of age since clearcutting (e.g., Yahner and Grimm 1984), on avifauna. A long-term management study for Ruffed Grouse (*Bonasa umbellus*) habitat consisting of a patchwork of one-ha even-aged stands in aspen (*Populus* spp.) and mixed-oak (*Quercus* spp.) cover types in central Pennsylvania (Liscinsky 1980) provided a unique opportunity to address two objectives: (1) to compare structure and seasonal dynamics of wintering and breeding avian communities among small even-aged stands of different age and cover type, and (2) to examine avian-habitat relationships in these small stands. General trends in avian abundance patterns between a large unmanaged sector and a large managed sector of the study area affected by

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the Ruffed Grouse management plan were investigated previously (Yahner 1984).

STUDY AREA

The study was conducted at the Barrens Grouse Habitat Management Study Area (BGMA), State Game Lands 176, Centre County, Pennsylvania, from December 1981 to June 1984. Major canopy trees on the study area include white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), bigtooth aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), and pitch pine (*Pinus rigida*). Principal understory and shrub species are scrub oak (*Q. ilicifolia*), dwarf chinkapin oak (*Q. muehlenbergii*), aspen, red maple (*Acer rubrum*), black cherry (*Prunus serotina*), and blueberry (*Vaccinium* spp.). Aspen cover is adjacent to an unimproved dirt road that bisects the BGMA in a northeast-southwest direction, whereas the mixed-oak cover type is about 400 m away from each side of the road. No streams or lakes occur at the BGMA, but a few temporary ponds are present.

The 1166 ha BGMA is divided into a control (unmanaged) and a treated (managed) sector of equal size. The treated sector is comprised of 136, 4-ha square blocks, each representing "activity centers" for Ruffed Grouse under the supervision of the Pennsylvania Game Commission. Sixty and 76 blocks are in aspen and mixed-oak cover types, respectively. A block is divided into four one-ha stands (100 × 100 m). The western stand in all blocks was cut in the winter 1976–77, and the northern stand in aspen blocks was cut only in the winter of 1980–81. Thus, aspen stands of three age classes and mixed-oak stands of two age classes are present on the treated sector, with 36% of this sector affected by clearcutting. The forest on the control sector and uncut stands on the treated sector are about 60 years old.

A total of 18 ha in six habitat "types" was selected for study. Types were distinguished on the basis of distance from clearcutting, age since clearcutting, and cover type. These included three one-ha stands on the control sector (hereafter termed control habitat), plus three one-ha stands each in uncut aspen (mature aspen habitat), western aspen (1976–77 aspen habitat), northern aspen (1980–81 aspen habitat), uncut mixed-oak (mature oak habitat), and western mixed-oak stands (1976–77 oak habitat) on the treated sector. Stands selected were representative of vegetative features and were >50 m from habitat disturbances created by the unimproved dirt road, restricted access roads, corridors along transmission powerlines, or frost pockets (additional details of each habitat type are presented in Yahner 1983a).

METHODS

Habitat sampling techniques.—Four random, 0.04-ha circular samples (James and Shugart 1970) were established in each one-ha stand for measurement of habitat variables in spring and summer 1982, of which two plots each were in a central and an edge zone (Yahner and Grimm 1984). The central zone was the 50 × 50 m interior portion of a stand, and the edge zone was the remaining 25-m wide border surrounding the central zone (after Strelke and Dickson 1980). Overstory tree (woody stem > 1.5 m tall, >7.5 cm dbh) variables included number of species and density (no./ha) and basal area (m^2/ha) of each species, of snags, and of all species and snags combined in the 0.04-ha sample. Understory tree (woody stem ≥ 1.5 m tall, 2.5–7.5 cm dbh) variables were number of species and density (no./ha) of each species and of all species combined in the 0.04-ha sample. Tall shrub (woody stem ≥ 1.5 m tall, <2.5 cm dbh) and short shrub (woody stem = 0.5–1.5 m tall, <2.5 cm dbh) variables were number of species and density (no./ha) of each species and of all species combined in two perpendicular, one-m wide transects in the 0.04-ha sample. Percent coverages of canopy, grasses and sedges combined, forbs, and total vegetation (grass, sedge, forb, and woody vegetation) at one m above ground were measured by taking 20 ocular tube sightings spaced at 2-m intervals along the transects. Growth-form diversity also was determined at the 20 sightings. This diversity was based on the presence of four growth forms (overstory trees, understory trees, short-tall shrubs, and herbs) and the Shannon index $H' = -\sum p_i \ln p_i$, where p_i is the proportion of sightings containing the ith growth form. Density (no./ha) of stumps (>0.25 m tall, >7.5 cm in diameter) and total length (m) of fallen logs (>3 cm in diameter) also were noted in each 0.04-ha sample. (Sampling methods, details of variables, and significant differences in variables among habitat types are given in Yahner and Grimm 1984.)

Avian sampling techniques.—Ten avian censuses were conducted each winter (late December–early March) and breeding season (late April–late June) for 3 consecutive years, giving 30 censuses per season in each habitat type. Censuses were conducted approximately once weekly; a similar census schedule was followed each year. All habitat types were censused on the same day (sunrise–10:30), and the order in which individual stands were visited per census was randomized. All birds seen or heard were recorded by observers who walked slowly along two 100-m transects spaced 50 m apart in each stand. Birds entering or leaving a stand were noted, but birds flying over the canopy were excluded (Conner and Dickson 1980).

Mean species richness (S), species diversity (H'), and total density were calculated per season in the six habitat types for all species combined and for three major foraging guilds, based on 30 censuses pooled over the three years. Combining data for each habitat type gave a better measure of avian habitat-use patterns and also increased sample size for statistical analyses compared to examining data from individual years (Rice et al. 1984). S is the total number of species; H' is based on the Shannon index, where p_i is the proportion of individuals of the ith species; and total density is the total number of individuals (no./10 ha) of all species combined. Major guilds were ground-shrub foragers (species typically foraging at ground level or <2 m above ground in vegetation), trunk-bark foragers (species typically foraging along main tree trunks or large branches), and sallier-canopy foragers (species typically foraging ≥2 m above ground in vegetation) (modified from Holmes et al. 1979, Swift et al. 1984). Mean density (no./10 ha) of individual species was determined per season in each habitat type. In addition, an importance value (IV) was derived for each major foraging guild and species per season in each habitat type (Kricher 1973, Yahner 1983b). An IV was the proportion of total censuses in which a foraging guild (or species) was recorded per season in a habitat type (×100) plus the relative mean total density (or mean species density) of a foraging guild (or species) per season in habitat type (×100) (maximum $IV = 200$); a foraging guild or species with an $IV \geq 75$ in either winter or the breeding season arbitrarily was classified as being an important component of the avian community in a given habitat type. The number of territories per foraging guild and species in each habitat type was determined during the breeding season using the spot-mapping technique (Williams 1936). A minimum of three contacts of a singing male was used to delineate territorial boundaries (IBCC 1970); partial territories (<50% with an individual stand) were estimated to the nearest 10%.

Mean S, H', and total density for all species combined and for each major foraging guild, as well as mean density for each common species (≥30 contacts in a given season), were compared among the six habitat types during winter and the breeding season using single-classification analyses of variance (ANOVA) and Kruskal-Wallis tests; a posteriori comparisons between habitat types were made with Student-Newman-Keuls and STP tests (Sokal and Rohlf 1981).

The six habitat types and 88 avian variables were considered as columns and rows, respectively, of a data matrix. Avian variables included mean and coefficient of variation (CV) of *S*, *H'*, and total density for all species combined and for each foraging guild; mean and CV of density for each common species in winter and the breeding season; cumulative numbers of all species combined and species per foraging guild in both winter and the breeding season; and cumulative number of territories for all species combined, each foraging guild, and each common species. These data were analyzed by *Q*-factor analysis (BMDP4M, Dixon 1981) to show associations among the six habitat types based on all avian population and community variables (after Yahner 1983b). A varimax (orthogonal) rotation was used, and factors were extracted by eigenvalues exceeding 0.5 (Rummel 1970).

Relationships between habitat variables and avian variables were analyzed with simple correlation analyses because of small sample size (N = six habitat types) and multicollinearity among habitat variables (after Dueser and Brown 1980, Yahner 1983b). If necessary, log-transformed data were used in correlation analyses to meet assumptions of the test (Sokal and Rohlf 1981).

RESULTS

Winter community structure.—The cumulative number of species per habitat type ranged from 1 to 9 during winter (Table 1). Mean *S*, *H'*, and total density for all species combined and for the trunk-bark foraging guild were higher in the three uncut than in the three clearcut habitats. The *IV* of the trunk-bark foraging guild exceeded 150 in each uncut habitat. Conversely, the ground-shrub foraging guild was poorly represented ($IV \leq 51$) in all habitat types, and no sallier- or canopy-foraging species were noted.

Of 13 wintering species (scientific names in Table 4) recorded in the six habitat types, only Black-capped Chickadees, Downy Woodpeckers, and White-breasted Nuthatches were common species (Table 2). These three species of trunk-bark foragers typically had a high *IV* in uncut habitats. Black-capped Chickadees were noted in all habitat types, and Downy Woodpeckers and White-breasted Nuthatches were absent only from 1980–81 aspen.

Breeding community structure.—The cumulative number of species observed per habitat types was much higher in the breeding season than in winter (Table 3). Mean *S* and *H'* for all species combined and for both the trunk-bark and sallier-canopy foraging guilds were generally highest in 1976–77 aspen and in uncut habitats. Mean total density and *IV* of trunk-bark and sallier-canopy foraging guilds were higher in the three uncut habitats compared to the three clearcut habitats. Conversely, mean *S* and total density for ground-shrub foragers were highest in 1976–77 aspen or 1976–77 oak habitats, or both. The *IV* of the ground-shrub foraging guild exceeded those of other guilds in all six habitat types.

Sixteen of the 69 species observed in the six habitat types during the breeding season were considered common species (Table 4). Rufous-sided

TABLE 1

CUMULATIVE NUMBER OF SPECIES, MEANS ± SD OF WINTER AVIAN COMMUNITY VARIABLES, AND IMPORTANCE VALUES OF GUILDS IN SIX HABITATS AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA DURING THREE WINTERS (1982–84)

Variable	Habitat type					
	Control	Mature aspen	1976–77 aspen	1980–81 aspen	Mature oak	1976–77 oak
Cumulative no. species:						
All species combined	7	8	8[a]	1	9	5
Ground-shrub forager	1	3	3	0	1	1
Trunk-bark forager	6	5	4	1	8	4
Species richness (*S*):						
All species combined[b]	1.8 ± 1.3†	1.2 ± 1.2†*	0.5 ± 0.7*	0.1 ± 0.2	1.3 ± 1.4†	0.6 ± 0.9*
Ground-shrub forager	0.1 ± 0.2	0.2 ± 0.5	0.1 ± 0.4	0.0 ± 0.0	0.1 ± 0.3	0.3 ± 2.8
Trunk-bark forager[b]	1.8 ± 1.2†	1.0 ± 1.0†*+	0.3 ± 0.7+§	0.1 ± 0.2§	1.2 ± 1.3†*	0.5 ± 0.8*+
Species diversity (*H'*):						
All species combined[b]	0.5 ± 0.5†	0.3 ± 0.4†*	0.1 ± 0.2*+	0.0 ± 0.0+	0.3 ± 0.4†*	0.1 ± 0.3*+
Trunk-bark forager[b]	0.5 ± 0.5†	0.2 ± 0.3†*	0.1 ± 0.2+	0.0 ± 0.0+	0.3 ± 0.4†	0.1 ± 0.2*+
Total density (no./10 ha):						
All species combined[b]	10.3 ± 11.2†	8.4 ± 9.8†*	2.2 ± 3.9*+	0.2 ± 1.2+	8.2 ± 11.1†*	3.3 ± 5.4*
Ground-shrub forager	0.1 ± 0.6	1.0 ± 2.7	0.8 ± 2.3	0.0 ± 0.0	0.4 ± 1.7	0.6 ± 1.0
Trunk-bark forager[b]	9.8 ± 9.0†	7.4 ± 9.1†*	1.9 ± 4.0+§	0.2 ± 1.2§	7.8 ± 11.0†*	2.7 ± 5.2*+
Importance value, *IV*:[c]						
Ground-shrub forager	23	51	44	0	23	32
Trunk-bark forager	200	155	48	7	159	58

[a] Includes one sighting of a Red-tailed Hawk (*Buteo jamaicensis*).

[b] Significant difference among habitat types; $\chi^2 \geq 11.07$, df = 5, $P < 0.05$; Kruskal-Wallis test. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; STP test.

[c] *IV* based on the sum of the proportion of total censuses (×100) in which a guild was present in a given habitat type (maximum = 24 censuses for trunk-bark foragers in control) and the relative density of a guild in a given habitat type (maximum density = 9.77/10 ha for trunk-bark foragers in control); maximum value of *IV* = 200.

TABLE 2

MEAN (± SD), DENSITY (NO./10 HA), AND IMPORTANCE VALUES FOR THREE SPECIES IN SIX HABITAT TYPES AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA DURING THREE WINTERS (1982–1984)

	Habitat type					
Species	Control	Mature aspen	1976–77 aspen	1980–81 aspen	Mature oak	1976–77 oak
Downy Woodpecker[a]	2.3 ± 2.5† (147)[b]	1.4 ± 2.4†* (82)	0.2 ± 0.8*+ (16)	0.0 ± 0.0 (0)	2.9 ± 3.8† (140)	0.1 ± 0.6*+ (8)
Black-capped Chickadee	4.3 ± 6.0†* (181)	5.0 ± 6.5† (188)	1.4 ± 3.4*+ (64)	0.2 ± 1.2+ (10)	3.3 ± 7.1†*+ (114)	1.6 ± 3.6*+ (66)
White-breasted Nuthatch	1.9 ± 2.6† (114)	0.7 ± 1.8†* (37)	0.1 ± 0.6* (8)	0.0 ± 0.0* (0)	0.6 ± 1.3†* (40)	0.1 ± 0.6* (8)

[a] Density of each species was significantly different among habitat types; $\chi^2 \geq 11.07$, df = 5, $P < 0.05$; Kruskal-Wallis test. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; STP test.

[b] Importance values (*IV*) are based on the sum of the proportion of total censuses (×100) in which a species was present in a given habitat type (maximum = 17 censuses for Downy Woodpecker in control) and the relative density of a species in a given habitat type (maximum density = 5.00/10 ha for Black-capped Chickadee in mature aspen); maximum *IV* = 200.

Towhees predominated (high density and *IV*) in all habitat types except 1980–81 aspen. Ovenbirds and Black-and-white Warblers seldom occurred in clearcut habitats. In contrast, Common Yellowthroats and Field Sparrows were characteristic of all three clearcut habitats. Gray Catbirds, Golden-winged Warblers, and Chestnut-sided Warblers were abundant in only older clearcut habitats, i.e., 1976–77 aspen and 1976–77 oak.

Breeding territories.—Most territories were established in 1976–77 aspen habitat, whereas few territories were located in 1980–81 aspen habitat (Table 5). Seventy percent of the total territories were those of ground-shrub foragers, which were located mainly in 1976–77 aspen and 1976–77 oak habitats. The remaining territories were established by trunk-bark and sallier-canopy foraging species, and these were positioned primarily in uncut habitats at the BGMA.

Relationships among habitat types.—Based on avian population and community variables, the six habitat types at the BGMA comprised two groups, corresponding to two factors extracted by factor analysis. Factor I associated the uncut habitats (factor loadings ≥ 0.86) and explained 81% of the variance. This factor, which is labeled a "breeding-season ground-shrub forager" factor, grouped habitat types characterized by unstable populations (high CV of mean density) of ground-shrub foraging species during the breeding season. For example, the CV of mean density for the Field Sparrow ranged from 227–381% in uncut habitats compared to only 61–141% in clearcut habitats.

Factor II, in contrast, grouped the three clearcut habitats and accounted for 15% of the variation. Factor II is termed a "winter-season trunk-bark forager" factor because the CV of both mean *S* and total density for the trunk-bark foraging guild and the CV of mean total density for the Black-capped Chickadees during winter in uncut habitats were much lower than those in clearcut habitats. For instance, the CV of mean total density for trunk-bark foragers varied from 195–548% in clearcut habitats versus only 92–141% in uncut habitats.

Winter avian-habitat relationships.—Avian variables, such as mean *S*, H', and total density for all species combined and for the trunk-bark foraging guild were positively correlated with habitat variables describing the vegetative structure of a relatively mature forest stand, including high overstory tree density, high growth-form diversity, and low understory tree and shrub densities (Table 6). Mean density of the three common species also was directly associated with these habitat variables. In contrast, mean *S*, H', and total density for the ground-shrub forager guild were directly correlated with high densities of understory trees, tall shrubs, and short shrubs, which represent vegetative structure typical of clearcut habitats.

TABLE 3

CUMULATIVE NUMBER OF SPECIES, MEANS (± SD) OF BREEDING AVIAN COMMUNITY VARIABLES, AND IMPORTANCE VALUES OF THREE GUILDS IN SIX HABITATS AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA DURING THREE SEASONS (1982–1984)

Variable	Habitat type					
	Control	Mature aspen	1976–77 aspen	1980–81 aspen	Mature oak	1976–77 oak
Cumulative no. species:						
All species combined	43	47	35[a]	16	51[b]	30
Ground-shrub forager	22	23	21	14	19	17
Trunk-bark forager	5	8	3	1	9	5
Sallier-canopy forager	16	16	10	1	21	8
Species richness (*S*):						
All species combined[c]	6.2 ± 3.6†*	8.8 ± 3.7+	8.0 ± 2.8†+	3.1 ± 1.9	6.8 ± 3.9†*	5.2 ± 2.1*
Ground-shrub forager[c]	3.7 ± 2.4†*	4.6 ± 2.1†	6.0 ± 2.1	3.0 ± 1.7*	3.2 ± 2.0*	4.2 ± 1.8†*
Trunk-bark forager[c]	1.3 ± 1.2†*	2.0 ± 1.1†	1.0 ± 0.8*	0.1 ± 0.3+	1.3 ± 1.2†*	0.3 ± 0.6+
Sallier-canopy forager[d]	1.5 ± 1.6†*	2.2 ± 1.5†	1.0 ± 0.9*	0.1 ± 0.3+	2.8 ± 1.7†	0.7 ± 0.8*+
Species diversity (*H′*):						
All species combined[c]	1.6 ± 0.5†*	1.9 ± 0.6+	1.8 ± 0.5†+	0.9 ± 0.6	1.7 ± 0.6†*+	1.4 ± 0.5*
Ground-shrub forager	1.0 ± 0.7	1.3 ± 0.6	1.6 ± 0.5	0.9 ± 0.5	0.9 ± 0.5	1.2 ± 0.5
Trunk-bark forager[d]	0.3 ± 0.5†*	0.5 ± 0.5†	0.2 ± 0.3*	0.0 ± 0.0+	0.3 ± 0.5†	0.0 ± 0.2*+
Sallier-canopy forager[d]	0.4 ± 0.6†*	0.7 ± 0.6†	0.2 ± 0.3*+	0.0 ± 0.0+	0.8 ± 0.7†	0.1 ± 0.3*+

TABLE 3
CONTINUED

Variable	Habitat type: Control	Mature aspen	1976–77 aspen	1980–81 aspen	Mature oak	1976–77 oak
Total density (no./10 ha):						
All species combined[c]	28.1 ± 19.8	42.3 ± 18.3	54.4 ± 20.6	21.5 ± 15.8	35.0 ± 21.0	39.6 ± 17.4
Ground-shrub forager[c]	15.2 ± 11.3†	23.8 ± 12.7†	45.0 ± 18.0	21.1 ± 15.5†	15.7 ± 9.4†	34.9 ± 16.8
Trunk-bark forager[d]	5.4 ± 4.8†*	10.0 ± 5.5	5.7 ± 5.3*	1.2 ± 5.5+	7.4 ± 8.0†*	1.8 ± 4.4+
Sallier-canopy forager[d]	7.6 ± 8.4†	8.6 ± 5.7†	3.9 ± 3.7*	1.2 ± 5.5+	12.3 ± 12.8†	3.0 ± 3.9*
Importance value (*IV*)[e]:						
Ground-shrub forager	131	146	200	140	128	173
Trunk-bark forager	85	119	86	12	84	24
Sallier-canopy forager	84	102	72	12	117	54

[a] Includes one sighting of a Great Horned Owl (*Bubo virginianus*).
[b] Includes one sighting each of a Red-tailed Hawk and a Great Horned Owl.
[c] Significant difference among habitat types; $F \geq 4.42$, df = 5,142, $P < 0.05$; single-classification ANOVA. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; Student-Newman-Keuls test.
[d] Significant difference among habitat types; $\chi^2 \geq 11.07$, df = 5, $P < 0.05$; Kruskal-Wallis test. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; STP test.
[e] An *IV* based on the sum of the proportion of total censuses (×100) in which a guild was present in a given habitat type (maximum = 30 censuses for ground-shrub forager in 1976–77 aspen) and the relative density of a guild in a given habitat type (maximum = 44.96/10 ha for ground-shrub forager in 1976–77 aspen); maximum value of *IV* = 200.

TABLE 4

MEAN (± SD), DENSITY (NO./10 HA), AND IMPORTANCE VALUE FOR 16 COMMON SPECIES IN SIX HABITAT TYPES AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA DURING THREE BREEDING SEASONS (1982–1984)

	Habitat type					
Species	Control	Mature aspen	1976–77 aspen	1980–81 aspen	Mature oak	1976–77 oak
Downy Woodpecker[a]	0.8 ± 1.7†*	1.2 ± 2.4†	0.0 ± 0.0*	0.2 ± 0.8†*	1.0 ± 2.8†*	0.1 ± 0.6†*
(*Picoides pubescens*)	(30)[b]	(42)	(0)	(9)	(25)	(5)
Blue Jay	0.9 ± 1.7†*	2.6 ± 4.3†	0.2 ± 0.8*	0.0 ± 0.0	4.8 ± 6.6†	0.2 ± 0.8*
(*Cyanocitta cristata*)	(36)	(74)	(9)	(0)	(111)	(9)
Black-capped Chickadee	2.6 ± 3.6†*+	4.2 ± 3.8†*	4.4 ± 4.6†	0.0 ± 0.0§	1.9 ± 3.6*+	1.1 ± 3.9+§
(*Parus atricapillus*)	(74)	(124)	(123)	(0)	(47)	(22)
Gray Catbird	0.0 ± 0.0†	0.9 ± 1.7†*	4.7 ± 4.3*+	1.1 ± 2.0†*	0.4 ± 1.2†	7.3 ± 5.6
(*Dumetella carolinensis*)	(0)	(35)	(121)	(41)	(25)	(163)
Red-eyed Vireo	1.9 ± 3.0†	1.2 ± 1.9†	0.0 ± 0.0*	0.0 ± 0.0*	1.0 ± 1.8†	0.4 ± 1.2†*
(*Vireo olivaceus*)	(60)	(49)	(0)	(0)	(44)	(19)
Black-and-white Warbler	0.4 ± 1.5†*+	3.1 ± 3.0§	1.1 ± 1.8†+	0.0 ± 0.0*	2.2 ± 2.9+§	0.2 ± 0.8†*
(*Mniotilta varia*)	(16)	(99)	(44)	(0)	(76)	(9)
Golden-winged Warbler	0.3 ± 1.0†	0.9 ± 2.1†*	4.6 ± 4.0+	0.6 ± 1.5†*	0.1 ± 0.6†	2.0 ± 2.3*+
(*Vermivora chrysoptera*)	(14)	(28)	(116)	(21)	(5)	(76)
Nashville Warbler	1.2 ± 2.2†	1.0 ± 1.8†	0.9 ± 1.7†*	0.0 ± 0.0*	0.7 ± 1.6†*	0.3 ± 1.8†*
(*Vermivora ruficapilla*)	(42)	(48*)	(35)	(0)	(21)	(27)
Chestnut-sided Warbler	0.4 ± 3.5†	0.9 ± 1.7†*	4.0 ± 3.8+	0.2 ± 0.8†	0.3 ± 1.0†	2.4 ± 3.0*+
(*Dendroica pensylvanica*)	(16)	(35)	(110)	(9)	(9)	(77)

TABLE 4
CONTINUED

Species	Habitat type					
	Control	Mature aspen	1976–77 aspen	1980–81 aspen	Mature oak	1976–77 oak
Ovenbird (*Seiurus aurocapillus*)	3.0 ± 2.5† (104)	3.2 ± 2.8† (103)	0.2 ± 0.8* (9)	0.0 ± 0.0* (0)	.9 ± 3.2† (120)	0.1 ± 0.6* (5)
Common Yellowthroat (*Geothlypis trichas*)	0.4 ± 1.2† (19)	0.9 ± 1.7† (35)	7.5 ± 6.3*+ (161)	3.6 ± 3.9* (106)	0.6 ± 1.3† (25)	8.4 ± 7.0+ (170)
Brown-headed Cowbird (*Molothrus ater*)	2.8 ± 3.8† (80)	2.0 ± 2.6† (72)	1.2 ± 2.4†* (42)	0.0 ± 0.0+ (0)	0.8 ± 1.7†*+ (30)	0.1 ± 0.6*+ (5)
Indigo Bunting (*Passerina cyanea*)	0.6 ± 1.3† (25)	1.1 ± 1.6† (48)	2.0 ± 2.4* (72)	0.8 ± 1.7† (30)	0.2 ± 0.8† (9)	1.6 ± 2.6 (49)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	2.1 ± 2.4†* (77)	6.3 ± 5.3+ (153)	9.9 ± 6.8+ (185)	6.1 ± 5.7†+ (143)	1.7 ± 2.3* (56)	9.9 ± 5.5+ (200)
Chipping Sparrow (*Spizella passerina*)	0.2 ± 0.8†* (9)	2.0 ± 2.9+ (64)	1.0 ± 1.8†+ (40)	0.2 ± 0.8†* (9)	0.0 ± 0.0* (0)	0.0 ± 0.0* (0)
Field Sparrow (*Spizella pusilla*)	0.7 ± 1.8†* (22)	0.6 ± 1.3†* (25)	7.4 ± 4.5+ (171)	8.1 ± 7.3+ (167)	0.3 ± 1.0† (9)	3.0 ± 4.2*+ (78)

[a] Density of each species was significantly different among habitat types; $\chi^2 \geq 11.07$, df = 5, $P < 0.05$; Kruskal-Wallis test. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; STP test.

[b] Importance values (*IV*) are based on the sum of the relative number of total censuses in which a species was present in a given habitat type (maximum = 27 censuses for Rufous-sided Towhee in 1976–77 oak) and the relative density of a species in a given habitat type (maximum = 9.88/10 ha for Rufous-sided Towhee in 1976–77 aspen and 1976–77 oak); maximum value of *IV* = 200.

TABLE 5

CUMULATIVE NUMBER OF TERRITORIES PER INDIVIDUAL SPECIES WITH >10 TERRITORIES, CUMULATIVE NUMBER OF TERRITORIES FOR ALL SPECIES COMBINED, CUMULATIVE PROPORTION (%) OF TOTAL TERRITORIES PER FORAGING GUILD, AND TOTAL NUMBER OF SPECIES ESTABLISHING BREEDING TERRITORIES (1982–1984)

	Habitat type						
	Control	Mature aspen	1976–77 aspen	1980–81 aspen	Mature oak	1976–77 oak	Total
No. territories per species:							
Gray Catbird	0.0	0.6	6.2	0.2	0.0	8.5	15.5
Black-and-white Warbler	0.5	5.0	1.5	0.2	3.0	0.4	10.6
Golden-winged Warbler	0.0	0.4	7.5	0.9	0.0	3.0	11.8
Chestnut-sided Warbler	0.2	0.2	6.0	0.4	0.2	4.0	11.0
Ovenbird	3.5	5.0	0.0	0.0	5.7	0.0	14.2
Common Yellowthroat	0.7	0.6	10.4	5.2	0.0	9.5	26.4
Indigo Bunting	0.5	0.9	4.6	1.4	0.2	2.5	10.1
Rufous-sided Towhee	1.6	5.1	8.5	4.6	2.2	7.5	29.5
Field Sparrow	0.5	0.0	7.7	5.0	0.2	2.5	15.9
Total no. territories, all species	24.4	38.1	61.3	18.5	29.3	39.7	211.3
% total no. territories, ground-shrub foragers	50	52	84	90	44	89	70
% total no. territories, trunk-bark foragers	16	22	6	2	17	9	12
% total no. territories, sallier-canopy foragers	34	26	10	8	39	2	18
No. species establishing territories	21	22	16	11	19	16	32

Several avian variables, including mean *S*, *H'*, and total density for the trunk-bark foraging guild and mean density for Downy Woodpeckers and Black-capped Chickadees, were directly associated with density and basal area of overstory *Populus, Quercus,* and snags. In contrast, mean *S*, *H'*, and total density for the ground-shrub foraging guild were positively correlated with short shrub densities of *Q. ilicifolia* and *Q. prinoides* combined and *P. serotina.*

Breeding avian-habitat relationships.—Several variables describing the total avian community, the trunk-bark foraging guild, and the sallier-canopy foraging guild were positively related to habitat variables, such as overstory tree density, canopy coverage, and growth-form diversity (Table 7). As in winter, the ground-shrub foraging guild was directly correlated with understory tree and tall shrub densities.

TABLE 6

CORRELATIONS BETWEEN VARIABLES DESCRIBING VEGETATIVE STRUCTURE AND THE AVIAN COMMUNITY OR POPULATIONS IN SIX HABITATS DURING THREE WINTERS (1982–1984)

	Vegetation variable					
Avian variable[a]	Density overstory trees	Basal area overstory trees	Density understory trees	Density tall shrubs	Density short shrubs	Growth-form diversity
Species richness (*S*):						
All species, $\bar{x}$	0.95*	0.90*			−0.92†	0.94*
All species, CV	−0.87*		−0.91†			−0.95*
Trunk-bark foragers, $\bar{x}$	0.95*	0.91*			−0.91*	0.90*
Trunk-bark foragers, CV	−0.92*	−0.82*	−0.83*			−0.95*
Species diversity (*H'*):						
All species, $\bar{x}$	0.89*	0.90*			−0.93*	0.83*
All species, CV	−0.91*				0.92†	
Trunk-bark foragers, $\bar{x}$	0.85*	0.86*			−0.95*	0.82*
Trunk-bark foragers, CV	−0.94†	−0.92†		0.91†	0.94†	
Total density:						
All species, $\bar{x}$	0.97*	0.93†			−0.91†	0.94*
All species, CV	−0.87*		−0.93†			−0.94*
Trunk-bark foragers, $\bar{x}$	0.97*	0.94†			0.94†	0.95*
Trunk-bark foragers, CV	−0.89*		−0.87*			−0.96*
Species density:						
Downy Woodpecker, $\bar{x}$	0.95†	0.97†			−0.92†	0.84*
Downy Woodpecker, CV	−0.93†	−0.93†		0.88†	0.88*	−0.98†
Black-capped Chickadee, $\bar{x}$	0.95*	0.88*				0.96*
Black-capped Chickadee, CV	−0.83*		−0.88†			−0.93*
White-breasted Nuthatch, $\bar{x}$		0.82*			0.92*	
White-breasted Nuthatch, CV	−0.96†	−0.95†		0.92†	0.97*	−0.92†

[a] Only significant correlations ($P < 0.05$) are included; a significant *r* is based on untransformed (†) or log-transformed (*) data; no sign designates a positive correlation, and a negative sign indicates a negative correlation.

TABLE 7

CORRELATIONS BETWEEN VARIABLES DESCRIBING VEGETATIVE STRUCTURE AND THE AVIAN COMMUNITY IN SIX HABITATS DURING THREE BREEDING SEASONS (1982–1984)

	Vegetation variable						
Avian variable[a]	Density overstory trees	Basal area overstory trees	Density understory trees	Density tall shrubs	Density short shrubs	Percent canopy coverage	Growth-form diversity
Cumulative no. species:							
All species	0.91*	0.82*	0.84*			0.96*	0.97*
Trunk-bark foragers	0.91*	0.91*			−0.91*	0.94†	
Sallier-canopy foragers	0.92*	0.85†	0.82*		−0.82*	0.98*	0.87*
Cumulative no. territories:							
All species			0.91†	0.91*			
Ground-shrub foragers			0.86†				
Trunk-bark foragers							0.90*
Sallier-canopy foragers	0.90†	0.91†				0.90*	0.96*
Species richness (*S*):							
All species, $\bar{x}$			0.87*				0.86*
All species, CV				−0.89*			
Ground-shrub foragers, $\bar{x}$				0.89†			
Trunk-bark foragers, $\bar{x}$							0.93*
Trunk-bark foragers, CV				−0.85†			−0.94†
Sallier-canopy foragers, $\bar{x}$	0.90†	0.91†				0.89*	0.92*
Sallier-canopy foragers, CV			0.94*			−0.87*	−0.91*

TABLE 7
CONTINUED

Avian variable[a]	Vegetation variable: Density overstory trees	Basal area overstory trees	Density understory trees	Density tall shrubs	Density short shrubs	Percent canopy coverage	Growth-form diversity
Species diversity (H'):							
All species, $\bar{x}$			0.89*				0.84†
All species, CV			−0.95†				−0.82†
Ground-shrub foragers, $\bar{x}$				0.88†			
Trunk-bark foragers, $\bar{x}$	0.83†	0.84*					0.87*
Sallier-canopy foragers, $\bar{x}$	0.92†	0.92†				0.82*	0.86*
Total density:							
All species, $\bar{x}$			0.82†	0.88*			
All species, CV				−0.87†			
Ground-shrub foragers, $\bar{x}$				0.86†	0.84*		
Ground-shrub foragers, CV				−0.87†			
Trunk-bark foragers, $\bar{x}$			0.82*			0.83*	0.95*
Trunk-bark foragers, CV			−0.82*				−0.95†
Sallier-canopy foragers, $\bar{x}$	0.93†	0.94†	0.83*			0.95*	0.96*
Sallier-canopy foragers, CV			−0.92*			−0.84*	−0.88*

[a] Only significant correlations ($P < 0.05$) are included; a significant r is based on untransformed (†) or log-transformed (*) data; no sign designates a positive correlation, and a negative sign indicates a negative correlation.

Density and basal area of overstory *Populus, Quercus,* and snags were directly correlated with mean *S, H'*, and total density for all species combined, as well as with the trunk-bark and sallier-canopy foraging guilds. Negative relationships were found between these avian variables and short shrub densities of *Q. ilicifolia* and *Q. prinoides* combined and *P. serotina.* In contrast, mean *S, H'*, and total density for ground-shrub foragers were positively associated with tall shrub densities of *Populus, Q. ilicifolia* and *Q. prinoides* combined, and *P. serotina.*

Mean density and cumulative number of territories of Downy Woodpeckers, Blue Jays, Red-eyed Vireos, Ovenbirds, and Brown-headed Cowbirds were positively correlated with several variables describing the structure of overstory trees (Table 8), and to density and basal area of individual overstory species (e.g., *Populus, Quercus, Carya, Pinus*), and snags. In comparison, mean density and cumulative number of territories of Common Yellowthroats, Rufous-sided Towhees, and Field Sparrows were inversely associated with these overstory structural and composition variables. Mean density and cumulative number of territories of a few species (e.g., Black-capped Chickadees) were positively related to total understory tree, tall shrub, or short shrub densities, and to densities of individual species (e.g., *Populus, Q. ilicifolia* and *Q. prinoides* combined, and *P. serotina*).

DISCUSSION

As in other northern latitudes, avifauna in all six habitat types at the BGMA was depauperate in winter compared to that during the breeding season (see Rotenberry et al. 1979). In contrast, avian density and diversity in southern latitudes of the United States peak during winter because of the presence of both permanent residents and a large number of wintering species that later migrate northward to breed (Dickson 1978). Moreover, habitats in southern regions have a milder climate and a greater abundance of food resources in winter relative to those in northern regions (Dickson 1978).

Greater density, diversity, and temporal stability of the wintering avian community, particularly the trunk-bark foraging guild, in uncut habitats at the BGMA suggest that resources (e.g., food and cover) were more abundant and predictable there than in early-successional, clearcut habitats (after Kricher 1975, Conner et al. 1979). Uncut habitats at the BGMA, characterized by abundant overstory trees and snags, provided cover and foraging substrata for wintering woodpeckers, nuthatches, and parids (see Conner et al. 1979, Briggs et al. 1982). Further, many overstory trees in uncut habitats are rough-barked *Quercus* and *Pinus,* which provide mast and seed as food as well as increasing the surface area upon which birds can forage for crevice-dwelling arthropods (Brawn et al. 1982). Black-capped Chickadees were best adapted to the wide range of habitat types at the BGMA during winter. Chickadees typically are abundant and widely distributed components of a wintering bird community (e.g., Back 1979, Conner et al. 1979) and are characteristic of both forest edges and interiors (Brewer 1963).

A lack of wintering ground-shrub foragers at the BGMA was partly due to a scarcity of weed seeds and the presence of snow or ice cover. Seed-producing forbs and grasses were primarily restricted to areas along the unimproved dirt road; snow and ice cover was present each winter during the study, which conceivably could increase energetic costs associated with foraging in either leaf litter or vegetation near ground level. Similarly, abundance and distribution of granivorous species or those that forage near ground level may be restricted in Midwest farmlands during winter due to these factors (Vance 1976; Yahner 1981, 1983b). Conversely, in even-aged stands of southern latitudes with limited or no snow cover, birds that forage at or near ground level are often the most abundant species in the wintering avian community (Hagar 1960, Blake 1982).

In contrast to avian community structure in winter, community structure in summer was not always more complex in older habitats at the BGMA. For example, species richness did not vary between 1976–77 aspen and uncut aspen habitats. Similarities in avian community structure among habitat types of different age were partially attributed to individual territories overlapping more than one stand. For instance, Black-capped Chickadees foraged primarily within portions of territories located in uncut aspen stands, but also foraged to a limited extent in contiguous 1976–77 aspen stands. Conversely, some species, such as Chestnut-sided Warblers, located most territories in clearcut habitats, yet used overstory trees as song perches along edges of proximal uncut habitats (see Strelke and Dickson 1980).

Species foraging at or near ground level during the breeding season are typically well represented in clearcut or selectively harvested forests (Franzreb and Ohmart 1978, Conner et al. 1979). In my study, high shrub density, which provided readily available foraging and nesting microhabitats for species such as Chestnut-sided Warblers and Rufous-sided Towhees partially accounted for high density, diversity, and temporal stability of the ground-shrub foraging guild in 1976–77 clearcut habitats. On the other hand, the trunk-bark and canopy-sallier foraging guilds were abundant and relatively stable in uncut compared to clearcut habitats at the BGMA, perhaps because uncut habitats contained overstory trees and snags as foraging and nesting sites (Crawford et al. 1981, Maurer et al. 1981).

TABLE 8

CORRELATIONS BETWEEN VARIABLES DESCRIBING VEGETATIVE STRUCTURE AND AVIAN POPULATIONS IN SIX HABITAT TYPES DURING THREE BREEDING SEASONS (1982–1984)

	Vegetation variable						
Avian variable[a]	Density overstory trees	Basal area overstory trees	Density understory trees	Density tall shrubs	Density short shrubs	Percent canopy coverage	Growth-form diversity
Downy Woodpecker, $\bar{x}$	0.94†	0.95*				0.83†	
Downy Woodpecker, T^b	0.99†	0.99†			−0.85*	0.95†	0.84†
Blue Jay, $\bar{x}$	0.88*	0.89*					
Blue Jay, T	0.95†	0.97*				0.84†	0.82*
Black-capped Chickadee, $\bar{x}$			0.86†				0.82*
Gray Catbird, T				0.85†			
Red-eyed Vireo, $\bar{x}$	0.96*	0.92*			−0.95†	0.97†	0.87*
Red-eyed Vireo, CV	−0.89*	−0.91*					
Red-eyed Vireo, T	0.98†	0.97*			−0.90*	0.99†	0.82*
Black-and-white Warbler, CV			0.94*	0.85*			
Golden-winged Warbler, $\bar{x}$				0.85†			
Golden-winged Warbler, T		−0.82*			0.82*		
Nashville Warbler, $\bar{x}$							0.92*
Nashville Warbler, T							0.87*
Chestnut-sided Warbler, $\bar{x}$				0.93†			
Chestnut-sided Warbler, CV				−0.95†			
Chestnut-sided Warbler, T				0.88†			

TABLE 8
CONTINUED

Avian variable[a]	Vegetation variable: Density overstory trees	Basal area overstory trees	Density understory trees	Density tall shrubs	Density short shrubs	Percent canopy coverage	Growth-form diversity
Ovenbird, $\bar{x}$	0.99†	0.99†			−0.83*	0.93†	0.85*
Ovenbird, T	0.98†	0.99*				0.87†	
Common Yellowthroat, $\bar{x}$	−0.88†	−0.95†			0.86*		
Common Yellowthroat, CV			−0.90†	−0.95*			
Common Yellowthroat, T	−0.92†	−0.97*			0.85†	−0.82†	
Brown-headed Cowbird, $\bar{x}$	0.83†	0.86*				0.88*	
Brown-headed Cowbird, T	0.90†				−0.89†	0.88†	0.87*
Indigo Bunting, CV				0.85†			
Indigo Bunting, T		−0.86*			0.84*		
Rufous-sided Towhee, $\bar{x}$	−0.83†	−0.85†			0.88†		
Rufous-sided Towhee, T					0.94*		
Field Sparrow, $\bar{x}$	−0.99*	−0.95*			0.82*	−0.93†	
Field Sparrow, CV	0.93†	0.95†			0.86*	0.90†	
Field Sparrow, T	−0.95*	−0.94*				−0.89*	

[a] Only significant correlations ($P < 0.05$) are included; a significant r is based on untransformed (†) or log-transformed (*) data; no sign designates a positive correlation, and a negative sign indicates a negative correlation.
[b] T = cumulative number of territories.

Rufous-sided Towhees presumably were best adapted to the various habitat types at the BGMA during the breeding season. This species is associated with forest edges or forests with dense understory (Forman et al. 1976, Casey and Hein 1983). At the BGMA, density of towhees was related to high density of certain shrub species (e.g., *Q. ilicifolia*) that were characteristic of both clearcut habitats and mature aspen habitat (Yahner and Grimm 1984). Several other common ground-shrub foragers, including Gray Catbirds, Golden-winged Warblers, Chestnut-sided Warblers, and Field Sparrows, probably also were benefited by the grouse habitat management study. These species typically occur in clearcut stands, forest openings, or forest edges with dense shrub or understory growth (Forman et al. 1976, Butcher et al. 1981, Crawford et al. 1981, Casey and Hein 1983). Red-eyed Vireos and Ovenbirds, however, which are examples of forest-interior species (Galli et al. 1976, Forman et al. 1976), apparently were unaffected by habitat fragmentation resulting from the current cutting cycle (see also Yahner 1984). Of the 16 common breeding species at the BGMA, eight species (Blue Jays, Black-capped Chickadees, Gray Catbirds, Red-eyed Vireos, Black-and-white Warblers, Chestnut-sided Warblers, Common Yellowthroats, Indigo Buntings) have showed significant population increases in Pennsylvania or in the eastern United States over the past couple of decades (Anderson et al. 1981). Conversely, two of the 16 species (Golden-winged Warblers and Rufous-sided Towhees) have shown recent statewide or regional declines (Anderson et al. 1981).

Conner et al. (1979) concluded that, in Virginia, large clearcut stands (20–30 ha) generally had a negative impact on avifauna, but that the effects of forest clearcutting on avian communities varied with season, seral stage, and bird species. At the BGMA, the mosaic of small, one-ha stands has increased vegetative diversity within a localized area, thereby attracting a variety of avian species adapted to different foraging and nesting microhabitats. No evidence is available to suggest that the grouse habitat management study has negatively impacted the distribution and abundance of wintering or breeding avifauna, although the effects of this plan on productivity due to nest predation or parasitism (see Whitcomb et al. 1981) have not been addressed. Yahner and Wright (1985), however, recently found that predation on artificial ground nests on the treated sector was less in both 1976–77 aspen and 1980–81 aspen habitats than in mature aspen habitat.

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