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Density and Diversity Responses of Summer Bird Populations to the Structure of Aspen and Spruce-Fir Communities on the Wasatch Plateau, Utah

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DENSITY AND DIVERSITY RESPONSES OF SUMMER BIRD POPULATIONS TO THE STRUCTURE OF ASPEN AND SPRUCE-FIR COMMUNITIES ON THE WASATCH PLATEAU, UTAH

by

Janet Lee Young

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Janet Lee Young

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Density and Diversity Responses of Summer Bird Populations

To the Structure of Aspen and Spruce-Fir Communities

On the Wasatch Plateau, Utah

by

Janet Lee Young, Doctor of Philosophy

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Major Professor: Dr. Keith L. Dixon
Department: Biology

Sixteen stands representing a range of structural variation in aspen, mixed aspen-conifer, and spruce-fir communities of the Wasatch Plateau, Utah, were censused by the sample count method. The stands were classified as eleven community types based on the understory dominants or indicator species and the cover types. Fifty bird species were recorded during the two seasons; thirty-two occurred in aspen cover, forty-four in mixed aspen-conifer cover, and twenty-two in spruce-fir.

Comparisons of the composition and density of bird populations were made between uniform stands of a single life form and more structurally complex stands of either single or mixed life forms. Limiting factors in the structural characteristics of the stands were identified for birds restricted to particular stands. Low avian similarities between some aspen stands were attributed to the differences in structure between the stands. Bird species which favored the deciduous life form tended to decrease in abundance in the mixed stands as the canopy coverage of conifers increased, and they were absent in the spruce-fir stand. Coniferous forest bird species were more abundant in mixed stands with high coniferous coverage than in the aspen-dominated stands. Low individual bird numbers were found in the conifer stand of uniform small trees.

Several vegetational characteristics of the stands were evaluated to determine if any was an index of forest heterogeneity predictive of bird species diversity. The habitat features of ecological relevance to most of the bird species were the size, spacing, and life form of the trees. The diversity of the distribution of diameter measurements at breast height for the tree species was predictive of bird species diversity. High diversity in the distribution of tree measurements at breast height was correlated with variation in tree height, tree canopy diameter, and the spacing of the life forms. It was therefore an index of three dimensional environmental patchiness, easily visualized by the variation in life forms and the number of stories within the stand.

(86 pages)

INTRODUCTION

Bird species often select and occupy a narrow range of vegetation types or specific life forms of plants during the breeding season. Their territorial behavior and conspicuousness allow for relatively accurate field determinations of population densities within different plant communities. Some bird species are exclusive to, or more often characteristic of, plant communities of a particular physiognomy whereas other bird species are more or less ubiquitous. Although some bird species respond differently to communities dominated by coniferous and deciduous life forms, avian populations are only seldom related to plant communities distinguished by the taxonomic composition of the plant dominants. Many bird species range freely not only throughout an entire plant community but far outside its limits.

Most North American studies directed toward determining bird populations have centered on censuses taken in pure stands only. However, Winternitz (1976) found high bird densities in Spruce/Aspen vegetation and Odum (1950) found higher bird population densities in mixed coniferous-hardwood forests than in deciduous forest. The mixed forest provided habitat both for species adapted to coniferous and to deciduous life forms. Thus the mixed forest could support more species than either pure deciduous or coniferous forest (Odum 1950).

This study presents population measurements in representative stands of uniform communities of a single life form and in more complex communities of both single and mixed life forms. By comparing the bird composition and population densities of these isolated, structurally defined pieces of the habitat, limiting factors in the structural characteristics of the stands could be identified for those bird species occurring in only particular stands. Similarly, the range of structural vegetational components of the habitat meeting the requirements of the non-restricted species also could be shown. The 16 stands censused represented a range of structural variation in aspen, mixed aspen-conifer, and spruce-fir communities resulting from the different climatic conditions on the various topographic aspects and from different histories. The stands varied in size, spacing (density), and life form of trees.

Studies of the relationships between stand physiognomy and avian diversity have demonstrated that as the vegetational complexity (measured in various ways) increases, the number of bird species also increases (MacArthur et al. 1962, Karr 1968, Recher 1969, Karr and Roth 1971, Willson 1974, and others). Balda (1969) and Laudenslayer and Balda (1976) found that the structure and complexity of the utilized habitat in addition to the total habitat potentially available must be measured to determine the relationship between bird species diversity and the structural complexity in some ecotones.

Studies in the eastern deciduous forest showed that the diversity of breeding bird species depended upon the foliage profile (percentage of vegetative cover, usually at three heights corresponding to herb, shrub, and canopy layers) and not upon plant species composition (MacArthur and MacArthur 1961). MacArthur et al. (1962) recognized the importance of internal variation within the vegetational profile but did not measure a horizontal component of habitat diversity. In applying his measures to the more complicated habitats of the mountain slopes in the western United States, MacArthur (1964) found that the number of layers of vegetation was no longer sufficient to account for bird species diversity when the areas included such major differences as patches of deciduous and coniferous forest. For many species the acceptability of the habitat apparently depended upon other variables such as availability of nest holes and water and the presence of oak or pine rather than on just the foliage profile.

Several other workers have been unable to find a correlation between bird species diversity (BSD) and foliage height diversity (e.g., Orians 1969, Terborgh and Weske 1969, Tomoff 1974, Wiens 1974, Willson 1974, and Carothers et al. 1974). Terborgh and Weske (1969) found the number of bird species in Peruvian forests to be more related to forest structure as determined by history than to the layering of the forest.

Roth (1976) devised a heterogeneity index, D (the coefficient of variation of distances derived from the point-centered quarter technique) which predicted BSD for a series of similar brushlands where other indices failed. There was no correlation, however, when the D-values for trees were used in forested areas. In this study several vegetational characteristics of the stands were evaluated to determine if any would provide an index of forest heterogeneity predictive of bird species diversity.

STUDY AREA

The state of Utah has been subdivided into three physiographic provinces with numerous subdivisions (Thornbury 1965) as illustrated in figure 1. The Middle Rocky Mountain region includes the Wasatch Mountains and the Uinta Range; the Colorado Plateau Province contains the High Plateaus Section, the Uinta Basin Section, and the Canyon Lands Section; the Basin and Range Province comprises the western one-third of the state. The study area is on the Wasatch Plateau of the High Plateaus Section (fig. 1).

All stands were at elevations of above 2400 m (8000 ft) and received an annual precipitation of 61-101 cm (24-40 in) (Pfister 1972). In this area the subalpine forest is broken by large meadows dominated by *Artemisia* which occupy the gentle basins of drainage systems.

Field work was conducted during the summers of 1973 and 1974. Sixteen study stands in Fairview Canyon, Sanpete County, Utah, were selected for their tree composition. The stands ranged from pure aspen, aspen-fir, aspen-spruce-fir, to spruce-fir. South-facing slopes were avoided because of microsite differences. All stands with aspen as their overstory dominant were on west to northwest-facing slopes except one (105) which had an aspect of 60° NE. Most mixed aspen-conifer stands were on northeast-facing slopes and the spruce-fir was on a north-facing slope.

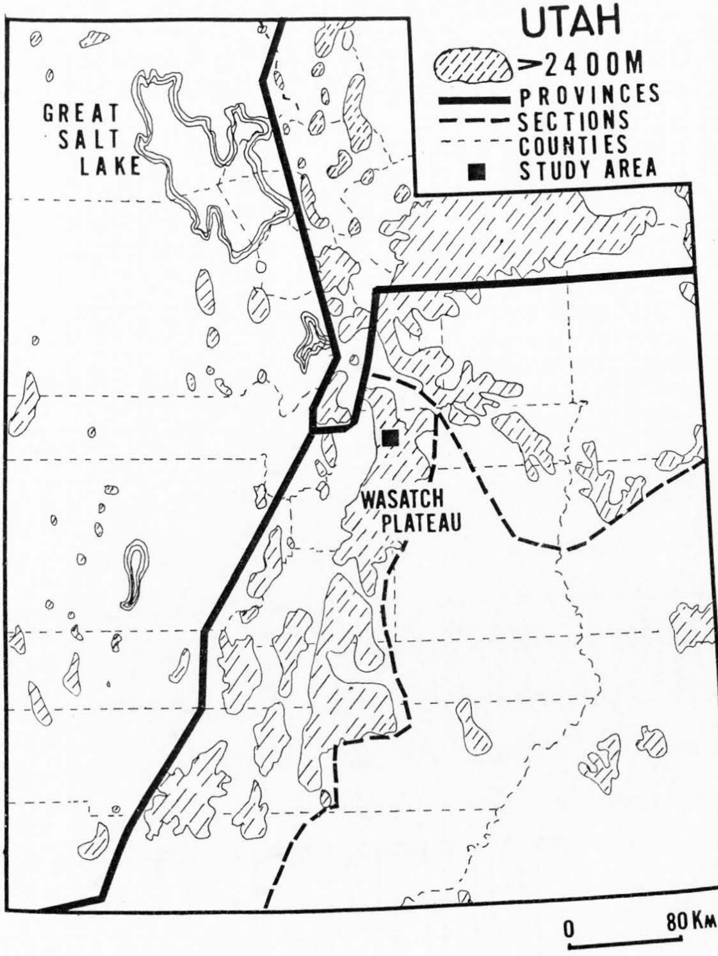

FIGURE 1. Location of study area and physiographic features of the state of Utah. Source: Thornbury 1965.

METHODS

Vegetation Sampling

In 1973 I used the point-centered quarter method of Cottam and Curtis (1956) to sample trees with a BDH of more than 2.54 cm (1 inch). Points were paced off at regular intervals of 15 or 25 meters, and at each point the surrounding area was divided into four quarters. The distance from the center point to the closest tree in each quarter was measured and the DBH of the tree was recorded. One hundred center points (400 trees) were recorded in structurally diverse stands and fewer points (25-75) were used in more uniform stands because the data became repetitious. The number of trees per 0.4 hectare was calculated for each stand.

During the summer of 1974, plots were placed within the stands to sample the ground vegetation, foliage height, and foliage volume. Grazing influence was onmipresent and no controls were attempted. On each plot (approximately 375 m^2 or 0.04 ha) the following data were recorded: (1) location, (2) elevation, (3) % slope, (4) aspect (Azimuth $^{\circ}$), (5) foliage height by classes; 0-1 m, 1-8 m, greater than 8 m, (6) total tree height by species, height from ground to lowest branches, and crown diameter for foliage volume calculations, (7) DBH by tree species, (8) tree age, (9) canopy coverage class for understory vegetation species (table 1), and (10) % canopy coverage of each overstory species.

A 15 by 25 m plot was laid out in a randomly selected area within each of the 16 stands. Corners of the macroplot were flagged and the ends were marked off at 5 and 10 m. Tapes were stretched between the two 5 m and the two 10 m end marks for sampling understory coverage. Fifty 20 by 50 cm microplots (fig. 2) were placed at 1 m intervals along

Table 1. Coverage classes used for understory vegetation.

Coverage classes	Percentage area covered	Midpoint of range
1	0- 5	2.5%
2	5- 25	15.0%
3	25- 50	37.5%
4	50- 75	62.5%
5	75- 95	85.0%
6	95-100	97.5%

(a "p" was recorded for individuals found within the plot but not sampled)

the two tapes (Daubenmire 1959). The understory canopy cover was measured by considering all individuals of one taxon in the microplot as a unit and assigning a coverage class with reference to the markings on the frame. The visual reference design painted on the frame equalled 5, 25, 50, 75, and 95% of the microplot area. In figure 3 the 71 mm^2 corner represents 5% of the frame, coverage class #1 (table 1). The alternating 12.5 cm by 20 cm white and black sections represent 25% each. Sections were summed to produce the 6 coverage classes. After sampling, the classes recorded for each taxon were transcribed to the midpoint value of each range (table 1), summed and then divided by the number of plots examined (50) to get the average coverage for the total area sampled (50 x 0.1 m = 5 m^2). This value was considered an estimate of average coverage for the whole stand (Daubenmire 1959).

Seventy voucher specimens were collected from all of the macroplots. They were identified by George M. Briggs at Utah State University and are deposited in the Intermountain Herbarium, Logan, Utah.

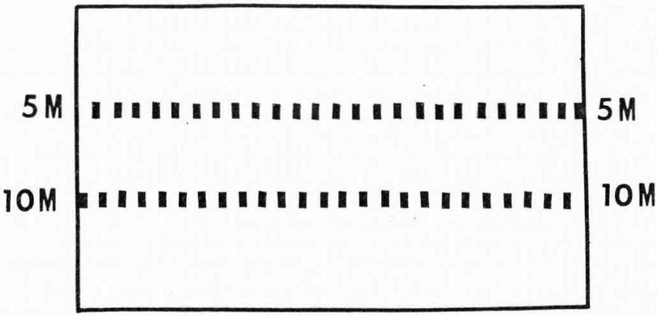

FIGURE 2. 15 by 25 m macroplot containing fifty 20 by 50 cm microplots placed at 1 m intervals. Source: Daubenmire 1959.

All tree species over 2.54 cm DBH within the 375 m^2 macroplot were recorded by diameter class. Diameter classes were recorded in inches; therefore each class added a 2.54 cm increment. All trees less than 2.54 cm DBH were recorded by species on two 1 by 25 m transects. All dead standing trees were tallied to appraise mortality trends. Representative trees of each species were measured for total tree height, height from ground to lowest dead branches if present, height from ground to canopy bottom, and crown radius. The shape of the crown for each tree was recorded as being conical, cylindrical, or spherical. A clinometer and tape were used for height measurements. The tree data were converted to total foliage volume per tree species (based on tree silhouette rather than the actual density of the foliage) and expressed by height from the ground. Foliage height and foliage volume diversities were calculated by using the percent of foliage present in each height class.

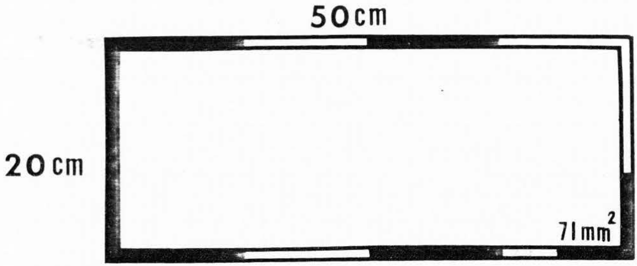

FIGURE 3. Visual reference design painted on microplot frame. Source: Daubenmire 1959.

Increment cores were taken for age determination of trees on each macroplot. Photographs were taken of each plot to illustrate the general physiognomy and composition of the stands.

Vegetation data from the macroplots were transcribed to an association table after the field work was completed. The stands were grouped according to their basic similarities in presence and percent cover of trees, shrubs, forbs, and graminoids.

The cover types for each of the 16 stands were determined by the percent of tree canopy cover in the macroplots. All tree species comprising 20% or more of the total combined coverage were recognized in naming the cover type. The cover types were subdivided into community types based on the understory dominants or indicator species (Henderson et al. 1977). The understory species used in the type name were based on a combination of fidelity, constancy (% occurrence) and dominance (% cover) within the community. Names for the community types were derived from the vernacular names of the overstory dominants and the scientific names for the understory vegetation. Species names for the different physiogonomic layers were separated by a slash(/) and two or more names within the same layer were separated by hyphens.

The stands were grouped into two series based on the overstory composition. The 100 series stands were comprised of only aspen whereas conifers were present on all of the 200 series stands. Stand 210 was comprised of only conifers and no aspen. Comparisons were made of the composition, size, and density of trees between the two series.

Bird Populations and Habitat Preferences

The bird populations were censused using the sample count method (Bond 1957). Each stand was censused twice each year during the breeding season, late June and early July. The breeding season at this elevation is short and apparently reaches a peak around the end of June. Censusing was always done between 05:30 (daylight) and 08:00, and no counts were made during a rain or high wind. The stands were close enough geographically that usually two were censused in one morning. The order of sampling the stands covered in one day was reversed on the second trip.

To make a sample count I entered a stand to a distance of about 45 meters and then stood still. I counted and recorded all the birds that I saw or heard beside or ahead of me for 5 minutes. Then I walked slowly for 5 minutes, averaging 135 meters, before recording for another 5 minutes. I tried not to count the same bird twice. This process was repeated until 5 census stops had been made.

After the two visits were made to a stand each year, the larger number of individuals per species was taken as the local population for that species. This method is the same as that used by Bond (1957) and similar to the method of Beals (1960). The validity of the population as determined by two trips to the census area has been evaluated by

Kendeigh (1944), and Bond (1957). Accuracy is approximately 70-80% of the individuals.

The strip census, strip map, point quarter, and sample count censusing methods were compared by Anderson (1972) to determine the best way to record and compare the avifaunal composition of both deciduous and coniferous sample plots. Anderson found that the sample count method gave a more accurate abundance index of the avian population than did the other methods.

If one assumes that individuals of a given species of bird act similarly in respect to their singing behavior and motor activity in the different stands in which they occur, then the sample count method should be valid for a comparative study of species between stands. The density figure is an "audiovisual" density index (Beals 1960) and is distinguished from absolute and relative density figures. The density data were not reduced to relative values because direct comparisons were desired between stands for each species. As Beals (1960) noted, comparisons between species within any particular stand must be made very cautiously because the species differ in their conspicuousness. No estimate of the number of birds per fixed unit area was attempted because no conspicuousness coefficients were assigned to the species and the area of each sample was indeterminate. An estimate of absolute density was not necessary for comparisons of populations between stands since all the stands were censused in the same manner.

The census results for the two summers were combined by taking the higher value for each species to minimize yearly fluctuations. This density index is distinguished from absolute density, relative density, mean density, and "audio-visual" density. The percent constancy for each bird species was figured based on yearly occurrence in each stand. Thus for a species to have a constancy of 100% it would have been recorded in all 16 stands both years.

The mean density index for each bird species was determined for the two stand series, 100 (aspen) and 200 (conifers present). The analysis of variance among the means of the series for each bird species was tested for significance by the F-test (Ostle 1963).

The following criteria were used to determine if a bird species which had a significant difference in its mean density indices between the two stands series demonstrated a habitat preference for one series: (1) if one or both means were equal to or less than 1.0, then one mean should be at least three times as great as the other; (2) if both means were greater than 1.0, then one mean should be at least twice as large as the other. A stricter test should be applied to species with low numbers because errors in measurement and random fluctuations attributable to factors other than choice produce a relatively greater disturbance in the data (Kendeigh 1974:22).

The abundance of bird species in a stand was determined from the census results. Abundance was calculated in three ways: the total number of bird species recorded for the two years (species richness); the mean number of species per census; and the mean number of species per census stop. The mean number of individuals per census stop also was calculated for each stand. Avian abundance was compared among stands, within and between community types, and between stand series. Correlations between the mean abundance measures were made to determine the relationships of the measures.

Correlation of Avifaunal and Vegetational Similarities

The similarity coefficient, $C = 2w/(a+b)$ where w is the sum of the lesser of the two values for each species in common between the two stands, a is the sum of all values in one stand, and b is the sum of all values for the other stand (Austin and Orloci 1966), was used to find the similarity indices for the bird and plant species. The density index for each bird species was used in the calculations. For the plant indices the percent cover for the understory plants and the density by DBH size class for tree species in the macroplots were used. Data for the trees were not reduced to the importance values of Curtis and McIntosh (1951) (the sum of relative values of frequency, density, and dominance) because such relative values are independent of distances and absolute densities per unit area (Cottam and Curtis 1956). The spacing of trees was considered important in this study as an indication of environmental patchiness. Also, if relative values had been used all pure aspen stands would have had the same value since only one tree species was present.

The correlation between the avian similarity and the vegetational similarity among the various stands was determined through the use of the similarity coefficients.

Statistical Data Analysis

The Shannon-Wiener information theory formula (Shannon and Weaver 1963) was used to calculate bird species diversity (BSD), plant species diversity (PSD), foliage height diversity (FHD), DBH diversity (DBHD), and distance diversity (DD). Foliage heights were for 0-1 m, 1-8 m, and greater than 8 m classes; DBH values were grouped by 2.54 cm intervals;

and distances from center points to trees were placed into 1 m intervals. Correlations between BSD and the measured vegetational and avian variables were determined and tested for significance by the F-test. Multiple regression analysis (Ostle 1963) was used to determine the extent each vegetational variable played in predicting BSD.

The computer programs used for the correlations, multiple regression analysis, and the analysis of variance among means were from the STAT PAC File at the Utah State University Computer Center. The species diversity program was provided by the Ecology Center, USU, and the HVAR program to test for significant differences between diversity indices (Hutcheson 1970) was programmed by Kim Marshall, USU. The association and constancy tables were run on the ASSOTAB program provided by Ron Mauk, USU.

RESULTS

Vegetation Stands

Features of the stands, including elevation, percent slope, numbers of trees, and percent understory cover are summarized in table 2. The understory plant species are coded and listed by decreasing constancy in table 3, and a constancy table including average percent coverage for the total species list is given in the Appendix.

Twenty-one understory species had a relative constancy of 75% or higher. Of these *Sambucus racemosa, Rudbeckia occidentalis,* and *Nemophila breviflora* are thought to be disturbance indicators (J. Henderson, pers. comm.). A summary of the important plant associations is given in table 4.

All 16 stands had more than 5% tree coverage and were therefore forest communities. The cover types were determined by the percent of the total tree coverage comprised of subalpine fir *(Abies lasiocarpa,* code "Abilas"), Engelmann spruce *(Picea engelmannii,* "Piceng"), and quaking aspen *(Populus tremuloides,* "Poptre"), as given in table 4. The 16 stands were classified as 11 community types (table 2) based on the understory dominants or indicator species and the cover type (tables 3, 4).

The stands were grouped into two series based on their overstory compositions for the analysis of avian habitat preference. The 100 series stands were comprised of aspen only whereas conifers were present on all 200 series stands. Stand 215 was classified as a QA/Rudocc plant community because less than 20% of its total tree coverage consisted of fir. However, it was grouped with the other mixed stands in the 200 series because it contained 19 subalpine fir trees per 0.4 ha.

TABLE 2. Some characteristics of the plant community stands.

Stand	Elevation (m)	Aspect	Slope (%)	Trees[a]/ 0.4 ha	Understory (% cover)	Trees[b]/50 m^2		Plant community type
						Aspen	Conifer	
105	2565	NE	20	332	75	6	0	Quaking aspen/*Symphoricarpos oreophilus*
111	2562	W	58	832	59	167	0	Quaking aspen/*Elymus glaucus*
112	2580	W	20	316	114	16	0	Quaking aspen/*Elymus glaucus*
103	2673	NW	10	71	53	1	0	Quaking aspen/*Rudbeckia occidentalis*
108	2673	NW	22	1152	131	2	0	Quaking aspen/*Rudbeckia occidentalis*
116	2808	NW	8	203	110	0	0	Quaking aspen/*Rudbeckia occidentalis*
109	2652	W	3	230	54	1	0	Quaking aspen/*Bromus* spp.
215	2829	NW	25	204	111	0	0	Quaking aspen/*Ribes montigenum*
202	2643	NE	15	150	73	10	0	Quaking aspen-Subalpine fir/ *Rudbeckia occidentalis*
204	2652	NW	19	271	71	3	0	Quaking aspen-Subalpine fir/ *Rudbeckia occidentalis*
207	2628	NW	16	300	114	24	0	Quaking aspen-Subalpine fir/ *Symphoricarpos oreophilus*
206	2640	NE	20	269	70	6	4	Subalpine fir-Quaking aspen/ *Ribes montigenum-Symphoricarpos oreophilus*
201	2640	N	10	207	31	6	25	Subalpine fir-Quaking aspen/*Ribes montigenum*
214	2817	NE	20	169	105	8	0	Subalpine fir-Quaking aspen/*Ribes montigenum*
213	2832	NE	15	115	50	0	2	Engelmann spruce-Subalpine fir-Quaking aspen/ *Ribes montigenum*
210	2613	N	55	731	33	0	161	Engelmann spruce-Subalpine fir/*Vaccinium caespitosum*

[a]Trees > 2.54 cm dbh.

[b]Trees < 2.54 cm dbh.

TABLE 3. Understory plant species (and code) by decreasing constancy in the 16 stands. See Appendix for average percent coverage for the total species list.

The species that had a constancy of 75% or more.

Bromus spp. (Bromus)	*Osmorhiza occidentalis* (Osmocc)
Chenopodium fremontii (Chefre)	*Poa reflexa* (Poaref)
Collomia linearis (Collin)	*Ranunculus inamoenus* (Ranina)
Descurania californica (Descal)	*Ribes montigenum* (Ribmon)
Galium biflorum (Galbif)	*Rudbeckia occidentalis* (Rudocc)
Hackelia floribunda (Hacflo)	*Sambucus racemosa* (Samrac)
Helenium hoopsii (Helhoo)	*Stellaria jamesiana* (Stejam)
Hydrophyllum capitatum (Hydcap)	*Thalictrum fendleri* (Thafen)
Lathyrus spp. (Lathyr)	*Valeriana occidentalis* (Valocc)
Nemophila breviflora (Nembre)	*Viola nuttallii* (Vionut)
Osmorhiza depauperata (Osmdep)	

The species that had a constancy of between 50 and 75%.

Achillea millefolium (Achmill)	*Melica spectabilis* (Melspe)
Agastache urticifolia (Agaurt)	*Mertensia arizonica* (Merari)
Agropyron spp. (Agrspp)	*Senecio serra* (Senser)
Erigeron speciosus (Erispe)	*Symphoricarpos oreophilus* (Symore)
Erythronium grandiflorum (Erygra)	*Taraxacum* spp. (Taraxa)

The species that had a constancy of between 25 and 50%.

Actaea rubra (Actrub)	*Geranium richardsonii* (Gerric)
Androsace septentrionalis (Andsep)	*Heracleum lanatum* (Herlan)
Aquilegia caerulea (Aqucoe)	*Lomatium dissectum* (Lomdis)
Aster engelmannii (Asteng)	*Phacelia hastata* (Phahas)

TABLE 3. Continued

Carex hoodii (Carhoo)	*Polemonium foliosissimum* (Polfol)
Collinsia parviflora (Colpar)	*Polygonum douglasii* (Poldou)
Delphinium barbeyi (Delbar)	*Potentilla* spp. (Potspp)
Delphinium nelsoni (Delnel)	*Viguiera multiflora* (Vigmul)
Elymus glaucus (Elygla)	*Viola canadensis* (Viocan)
Epilobium angustifolium (Epiang)	

The species that had a constancy of between 10 and 25%.

Bromus ciliatus (Brocil)	*Madia glomerata* (Madglo)
Carex geyeri (Cargey)	*Mitella stauropetala* (Mitsta)
Castilleja rhexifolia (Casrhe)	*Penstemon whippleanus* (Penwhi)
Claytonia lanceolata (Clalan)	

The species that had a constancy of less than 10%.

Arnica cordifolia (Arncor)	*Phleum alpinum* (Phlalp)
Castilleja spp. (Casspp)	*Poa pratensis* (Poapra)
Fragaria spp. (Fragar)	*Pyrola secunda* (Pyrsec)
Galium boreale (Galbor)	*Smilacina stellata* (Smiste)
Haplopappus spp. (Haplop)	*Tragopogon dubius* (Tradub)
Lupinus spp. (Lpinus)	*Vaccinium caespitosum* (Vaccae)
Pachistima myrsinites (Pacmyr)	

TABLE 4. Summary association table giving average percent coverage for important species in plant community types. Important associations within a community type are underlined. Refer to Table 3 for code names.

	Community type[a] and stand number															
Species	QA/ Symore	QA/Elygla		QA/Rudocc			QA/ Bromus	QA/ Ribmon	QA-SAF/ Rudocc		QA-SAF/ Symore	SAF-QA/ Ribmon-Symore	SAF-QA/ Ribmon		ES-SAF-QA/ Ribmon	ES-SAF/ Vaccae
Code	105	111	112	103	108	116	109	215	202	204	207	206	201	214	213	210
Trees																
Abilas	*	*	*	*	*	*	*	5.0	10.0	17.0	15.0	23.0	50.0	15.0	15.0	20.0
Piceng	*	*	*	*	*	*	*	*	*	*	*	*	*	0.3	25.0	65.0
Poptre	60.0	80.0	60.0	23.0	60.0	50.0	55.0	70.0	30.0	40.0	35.0	10.0	13.0	15.0	10.0	*
Shrubs																
Pacmyr	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	2.0
Ribmon	*	2.0	0.3	*	0.3	0.3	*	47.0	0.3	0.3	1.0	8.0	3.0	26.0	8.0	0.3
Samrac	*	*	0.3	*	33.0	16.0	1.0	7.0	14.0	4.0	13.0	0.3	3.0	18.0	0.3	*
Symore	7.0	0.3	1.0	*	*	*	0.3	5.0	*	*	8.0	7.0	*	*	*	0.3
Vaccae	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	8.0
Graminoids																
Agrspp	1.0	0.3	0.3	1.0	0.3	1.0	2.0	0.3	*	0.3	*	*	*	0.3	*	*
Bromus	1.0	*	4.0	2.0	2.0	2.0	6.0	0.3	1.0	2.0	0.3	*	*	2.0	0.3	*
Elygla	*	7.0	11.0	*	1.0	*	*	*	1.0	4.0	1.0	1.0	*	*	*	*
Forbs																
Lathyr	5.0	24.0	9.0	7.0	1.0	2.0	4.0	2.0	4.0	1.0	1.0	3.0	1.0	0.3	4.0	1.0
Nembre	1.0	0.3	1.0	1.0	1.0	13.0	0.3	1.0	6.0	2.0	0.3	1.0	1.0	1.0	*	*
Rudocc	9.0	*	12.0	14.0	14.0	24.0	2.0	6.0	10.0	12.0	4.0	4.0	0.3	9.0	2.0	*

[a]Code to community cover types: QA = quaking aspen; SAF = subalpine fir; ES = Engelmann spruce.

Comparisons of tree sizes and densities for the two series are presented in table 8. The number of aspen per 0.4 ha was significantly higher in the 100 series stands whereas the number of fir was significantly higher in the 200 series. However, the total number of trees per 0.4 ha was not significantly different between the two series. The maximum tree DBH and maximum DBH of fir also were significantly different between the two series; the larger trees occurred in the 200 series stands. However, the maximum DBH of aspen was not significantly different between the two series.

Bird Species Richness

The census results for each year are given in table 5. Species are listed by decreasing relative constancy (% occurrence). Fifty species were recorded during the two seasons; 88% of these were present in 1973 and 92% in 1974. The number of species recorded in each stand was fairly constant for the two years although the species varied. The greatest yearly change in number of species occurred in stands 204 and 207; both showed an increase of more than 40% the second year. The species responsible for these large increases had low "audio-visual" densities and six of the additional species in 1974 occurred in both of the stands. The increases were not a function of the censusing procedure because all of the stands were censused identically both years.

The bird species richness of the different cover types is compared in table 6. The greatest number of species occurred in the mixed aspen-conifer cover each year.

The abundance of bird species in a stand was calculated in three ways: species richness, the total number of bird species recorded on

TABLE 5. Yearly census results[a] for all bird species recorded listed by decreasing relative constancy.

Species	Const. (%)	QA/ Symore		QA/Elygla				QA/Rudocc					
		105		111		112		103		108		116	
		1973	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74
Turdus migratorius	100	4	8	9	12	9	11	7	9	8	7	10	2
Dendroica coronata	100	2	5	4	7	5	5	4	3	10	5	5	3
Junco caniceps	100	2	6	9	6	8	5	5	5	5	7	3	7
Selasphorus platycercus	97	2	2	3	3	6	5	2	2	4	4	0	3
Troglodytes aedon	94	8	8	8	6	14	8	9	12	1	2	7	2
Spinus pinus	91	0	1	0	3	5	5	1	2	1	2	8	6
Vireo gilvus	91	6	7	9	13	10	9	4	5	6	2	5	4
Contopus sordidulus	91	3	3	4	5	6	4	4	3	1	2	5	3
Zonotrichia leucophrys	84	14	11	4	1	15	8	5	0	27	19	23	18
Iridoprocne bicolor	84	5	2	2	2	12	3	21	14	4	1	1	1
Empidonax oberholseri	75	2	2	1	0	2	2	0	1	1	0	2	0
Sphyrapicus varius	75	0	2	0	3	2	2	4	2	1	1	-	-
Colaptes auratus	69	2	1	0	2	0	2	4	7	0	1	1	0
Parus atricapillus	69	0	1	0	1	1	1	-	-	-	-	-	-
Piranga ludoviciana	66	-	-	2	0	1	0	-	-	0	1	-	-
Carpodacus cassinii	63	1	2	-	-	1	2	0	3	-	-	1	2
Zenaida macroura	50	2	4	-	-	1	2	0	1	-	-	-	-
Regulus calendula	50	-	-	-	-	-	-	-	-	-	-	-	-
Passerina amoena	47	1	3	-	-	3	1	-	-	0	2	3	2

Species	QA/ Bromus		QA/ Ribmon		QA-SAF/Rudocc				QA-SAF/ Symore		SAF-QA/ Ribmon-Symore		SAF-QA/Ribmon				ES-SAF-QA/ Ribmon		ES-SAF/ Vac[illegible]	
	109		215		202		204		207		206		201		214		213		210	
	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74
Turdus migratorius	6	6	9	5	14	9	7	8	8	7	6	9	7	9	6	10	5	7	5	5
Dendroica coronata	6	3	5	5	7	9	4	8	6	6	5	7	5	6	3	4	2	5	7	5
Junco caniceps	7	10	8	5	6	6	4	9	4	5	8	10	8	7	11	11	12	9	4	5
Selasphorus platycercus	1	4	3	4	1	3	1	2	1	3	1	3	1	2	1	5	6	6	3	4
Troglodytes aedon	6	7	7	5	8	7	2	2	4	4	4	2	7	6	2	5	0	1	0	3
Spinus pinus	0	2	13	6	6	3	5	6	13	14	5	14	1	5	6	6	7	16	6	2
Vireo gilvus	9	5	3	5	3	5	2	4	3	3	2	4	4	3	1	3	0	1	-	-
Contopus sordidulus	4	4	4	3	5	5	4	3	4	3	5	6	5	5	2	2	0	2	-	-
Zonotrichia leucophrys	11	11	16	10	0	1	3	3	8	11	5	9	1	1	12	12	6	0	-	-
Iridoprocne bicolor	7	6	3	1	11	9	0	2	2	2	0	2	9	7	1	1	1	0	-	-
Empidonax oberholseri	2	1	2	0	1	2	1	1	2	1	1	2	2	2	1	0	1	0	1	0
Sphyrapicus varius	-	-	1	1	2	2	0	2	1	2	4	2	3	2	2	0	1	1	1	1
Colaptes auratus	2	1	0	1	3	3	2	1	-	-	1	0	3	3	1	1	0	1	0	1
Parus atricapillus	0	1	1	1	3	3	3	2	3	3	2	4	0	4	3	4	5	10	6	3
Piranga ludoviciana	2	1	3	2	5	1	0	2	0	3	1	3	2	2	6	5	3	4	2	1
Carpodacus cassinii	2	4	1	4	0	2	0	2	0	4	2	3	0	2	0	4	2	1	-	-
Zenaida macroura	4	2	-	-	0	3	0	2	0	2	4	9	0	3	1	1	0	3	-	-
Regulus calendula	-	-	0	1	1	4	5	6	3	5	8	8	4	6	2	2	3	7	0	3
Passerina amoena	-	-	3	7	-	-	-	-	-	-	0	1	-	-	2	3	2	1	1	0

[a]Dash indicates not recorded either year.

TABLE 5. (Continued)

Species	Const. (%)	QA/ Symore		QA/Elygla				QA/Rudocc						QA/ Bromus		QA/ Ribmon		QA-SAF/Rudocc				QA-SAF/ Symore		SAF-QA/ Ribmon-Symore		SAF-QA/Ribmon				ES-SAF-QA/ Ribmon		ES-SAF/ Vaccae	
		105		111		112		103		103		116		109		215		202		204		207		206		201		214		213		210	
		1973	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74
Catharus ustulatus	47	1	0	-	-	1	0	-	-	-	-	-	-	-	-	-	-	0	1	4	1	0	1	3	1	1	2	1	1	1	0	1	1
Catharus guttatus	47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	3	3	3	3	1	4	3	3	3	2	2	2	1	2	3
Pheucticus melanocephalus	44	0	2	2	2	2	1	3	1	2	0	1	0	2	0	-	-	1	0	-	-	0	1	-	-	-	-	1	1	-	-	-	-
Parus gambeli	38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	0	1	0	1	0	2	2	2	8	4	2	8	0	1
Spizella passerina	34	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	0	2	1	2	-	-	3	4	2	1	1	3	0	2	-	-
Regulus satrapa	34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	4	0	2	1	6	0	3	1	1	2	5	1	1
Molothrus ater	28	-	-	1	0	1	0	-	-	0	2	-	-	3	0	-	-	1	0	0	1	0	3	0	1	0	3	-	-	-	-	-	-
Bubo virginianus	28	1	1	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-	1	1	1	0	0	1	1	0	-	-	1	0	-	-
Sitta canadensis	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	4	0	2	-	-	1	2	3	2	1	1
Dendrocopos villosus	25	-	-	-	-	0	1	0	1	-	-	0	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	1	3	1	0	-	-
Nuttallornis borealis	25	1	0	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-	2	1	1	1	-	-	0	1	0	1	-	-
Progne subis	22	-	-	-	-	-	-	0	10	-	-	-	-	0	1	-	-	-	-	1	2	0	1	-	-	1	2	-	-	-	-	-	-
Sialia currucoides	22	1	0	-	-	-	-	1	1	-	-	5	2	2	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melospiza melodia	19	-	-	-	-	0	5	-	-	0	2	2	0	-	-	-	-	-	-	-	-	0	1	-	-	-	-	2	3	-	-	-	-
Empidonax difficilis	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	1	3
Dendroica petechia	13	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	1	0	-	-	-	-	-	-	1	0	-	-	-	-	-	-
Oporornis tolmiei	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	-	-	1	0	-	-	-	-	0	1	0	3	-	-
Cyanocitta stelleri	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	2	1	0
Dendrocopos pubescens	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	1	1	-	-	-	-

TABLE 5. (Continued)

Species	Const. (%)	QA/ Symore		QA/Elygla				QA/Rudocc						QA/ Bromus		QA/ Ribmon		QA-SAF/Rudocc				QA-SAF/ Symore		SAF-QA/ Ribmon- Symore		SAF-QA/Ribmon				ES- SAF-QA/ Ribmon		ES-SAF/ Vaccac	
		105		111		112		103		108		116		109		215		202		204		207		206		201		214		213		210	
		1973	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74	'73	'74
Wilsonia pusilla	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-
Accipiter striatus	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2
Nucifraga columbiana	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	0	3	-	-
Tachycineta thalassina	3	-	-	-	-	-	-	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Buteo swainsoni	3	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chordeiles minor	3	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dendragapus obscurus	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sitta carolinensis	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-
Sphyrapicus thyroideus	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0	-	-	-	-
Certhia familiaris	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-
Pinicola enucleator	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0	-	-
Bonasa umbellus	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	[illegible]
Total no. species/year		18	19	13	14	21	21	15	20	13	16	16	14	17	20	18	21	21	23	18	26	19	28	22	27	22	25	30	32	23	25	17	19
Total no. species		22		17		24		22		18		18		22		22		28		26		30		28		28		36		32		22	

TABLE 6. Avifaunal comparison of cover types and series.

Species	Total	No. of species in: Aspen (100 series)	Aspen-conifer	Spruce-fir	200 series
All observed 1973	44	27 (61%)	40 (91%)	17 (39%)	41 (93%)
All observed 1974	46	29 (63%)	40 (87%)	19 (41%)	42 (91%)
Total observed	50	32 (64%)	44 (88%)	22 (44%)	46 (92%)
Exclusive to cover type	15 (30%)	4 (08%)	9 (18%)	2 (04%)	
Exclusive to series	22 (44%)	4 (08%)			18 (36%)

the stand for two years; the mean number of species per census; and the mean number of species per census stop. These abundance figures, plus the mean number of individuals per census stop, and the bird species diversity for each stand are given in table 7. Avian abundance was not more similar within plant community types than between community types. The correlation between the mean abundance measures per census stop was high ($r = .9018$, $p < .001$, 15 d.f.) and correlations among all of the abundance measures were significant at the .001 level. Stand 112 had the highest values of the pure aspen series whereas stands 108 and 111 were consistently low. In general the values were higher for the 200 series than for the 100 series. The obvious exception was stand 210 which lacked aspen and had the lowest number of individuals per census stop.

The differences in bird species richness and mean bird numbers per census between the aspen and the mixed stands are given in table 8. Comparisons of species abundance between the two series were significantly different.

TABLE 7. Abundance and diversity of bird species in each stand.

Stand	Community	Total no. bird species	Mean number Spp./ census	Spp./ census stop	Individuals/ census stop	Diversity index H'	Variance
105	QA/Symore	22	13.8	6.7	9.2	2.577	.037
111	QA/Elygla	17	10.8	5.9	9.7	2.327	.042
112		24	16.8	8.9	13.8	2.728	.025
103	QA/Rudocc	22	14.3	7.4	12.4	2.526	.038
108		18	11.5	5.6	9.9	2.158	.068
116		18	13.3	6.6	10.7	2.323	.057
109	QA/Bromus	22	14.0	7.6	11.6	2.637	.029
215	QA/Ribmon	22	15.0	7.8	11.5	2.646	.030
202	QA-SAF/ Rudocc	28	17.3	9.2	13.2	2.819	.027
204		26	17.8	8.0	11.2	2.909	.024
207	QA-SAF/Symore	30	19.8	9.1	13.0	2.931	.025
206	SAF-QA/Ribmon-Symore	28	19.8	9.6	14.1	2.972	.019
201	SAF-QA/Ribmon	28	19.0	8.5	11.6	3.001	.020
214		36	23.0	9.6	14.0	3.033	.028
213	ES-SAF-QA/ Ribmon	32	19.8	8.6	12.8	2.958	.026
210	ES-SAF/Vaccae	22	13.5	5.6	6.5	2.707	.029

TABLE 8. Statistical differences between pure aspen stands (100 series) and stands in which conifers were present (200 series).

Variable	Stand series[a]		
	$\bar{X}$ 100	$\bar{X}$ 200	$F\text{-ratio}_{15\ d.f.}$
Total no. bird species	20.43	28.00	15.513**
Mean no. bird species/census	13.46	18.31	14.804**
Mean no. bird species/census stop	6.94	8.42	6.079*
Mean no. bird individuals/ census stop	11.01	11.98	.877
Number trees/0.4 ha (1 acre)	448.00	268.44	1.488
Number aspen/0.4 ha	448.00	119.56	6.171*
Number fir/0.4 ha	0.00	88.00	13.260**
Number spruce/0.4 ha	0.00	62.89	.846
Maximum DBH (any tree species)	50.11 cm (19.73 in)	78.26 cm (30.81 in)	9.125**
Maximum DBH of aspen	50.11 cm (19.73 in)	52.48 cm (20.66 in)	.054
Maximum DBH of fir	0.00 0.00	75.62 cm 29.77 in)	98.190**
Maximum DBH of spruce	0.00 0.00	14.66 cm (5.77 in)	1.301

[a] $\bar{X}$ = mean for series; * = $p < .05$; ** = $p < .01$

Habitat Preferences

There was a 44% difference between the two series with 4 and 18 species exclusive to the 100 and 200 series, respectively (table 6). The population densities of several species also were significantly different between the two series (table 9). In other words the series differed quantitatively as well as qualitatively.

Several bird species were found exclusively in a particular type. Four species: Mountain Bluebird *(Sialia currucoides)*, Violet-green Swallow *(Tachycineta thalassina)*, Swainson's Hawk *(Buteo swainsoni)*, and Common Nighthawk *(Chordeiles minor)* were recorded only in aspen stands whereas two species: Sharp-shinned Hawk *(Accipiter striatus)* and Ruffed Grouse *(Bonasa umbellus)* were recorded only in the spruce-fir stand. Nine species: MacGillivray's Warbler *(Oporornis tolmiei)*, Downy Woodpecker *(Dendrocopos pubescens)*, Wilson's Warbler *(Wilsonia pusilla)*, Clark's Nutcracker *(Nucifraga columbiana)*, Blue Grouse *(Dendragapus obscurus)*, White-breasted Nuthatch *(Sitta carolinensis)*, Williamson's Sapsucker *(Sphyrapicus thyroideus)*, Brown Creeper *(Certhia familiaris)*, and Pine Grosbeak *(Pinicola enucleator)* were found only in the mixed aspen-conifer stands.

All of the species exclusive to a cover type, except the Mountain Bluebird, had low "audio-visual" densities and the majority were recorded only one of the two years in any particular stand.

The species exclusive to aspen cover occurred in stands 103 (three species), 109 (2 species), 105 and 116 (1 species each). The occurrence of species exclusive to mixed aspen-conifer cover was as follows: four species in stand 214; two species each in 202, 207, and 213; and one

TABLE 9. Population responses of all bird species to the overstory composition of the stand series. Relative constancy is given for each species.

Species that exhibited a statistically significant population response to the 100 series stands.

Troglodytes aedon (94)	*Pheucticus melanocephalus* (44)
Vireo gilvus[a] (91)	*Sialia currucoides* (22)

Species that had a significant population response to the 200 series stands.

Spinus pinus (91)	*Catharus guttatus*[b] (47)
Parus atricapillus (69)	*Parus gambeli*[b] (38)
Piranga ludoviciana (66)	*Spizella passerina* (34)
Regulus calendula[b] (50)	*Regulus satrapa*[b] (34)
Catharus ustulatus (47)	*Sitta canadensis*[b] (28)

Species that showed no significant population difference between the two series.

Turdus migratorius (100)	*Melospiza melodia* (19)
Dendroica coronata (100)	*Empidonax difficilis*[b] (13)
Junco caniceps (100)	*Dendroica petechia* (13)
Selasphorus platycercus (97)	*Oporornis tolmiei*[b] (13)
Contopus sordidulus[a] (91)	*Cyanocitta stelleri*[b] (13)
Zonotrichia leucophrys[a] (84)	*Dendrocopos pubescens*[b] (9)
Iridoprocne bicolor[a] (84)	*Wilsonia pusilla*[b] (9)
Empidonax oberholseri (75)	*Accipiter striatus*[b] (6)
Sphyrapicus varius (75)	*Nucifraga columbiana*[b] (6)
Colaptes auratus (69)	*Tachycineta thalassina* (3)
Carpodacus cassinii (63)	*Buteo swainsoni* (3)
Zenaida macroura (50)	*Chordeiles minor* (3)
Passerina amoena (47)	*Dendragapus obscurus*[b] (3)
Molothrus ater (28)	*Sitta carolinensis*[b] (3)
Bubo virginianus (28)	*Sphyrapicus thyroideus*[b] (3)
Dendrocopos villosus (25)	*Certhia familiaris*[b] (3)
Nuttallornis borealis (25)	*Pinicola enucleator*[b] (3)
Progne subis (22)	*Bonasa umbellus*[b] (3)

[a]Recorded on all stands except 210 (ES-SAF/Vaccae).

[b]Recorded only on stands of the 200 series.

species in stand 215. Thus all of the species exclusive to a particular cover type were not found in any one stand.

The stands supported three general groups of birds: species which showed no significant population response to the different tree compositions of the stands; species that had higher population densities in pure aspen stand; and ones with higher densities in stands where conifers were present.

Common species which showed no significant difference in their mean density indices between the two series included the American Robin *(Turdus migratorius)*, Yellow-rumped (Audubon's) Warbler *(Dendroica coronata)*, Gray-headed Junco *(Junco caniceps)*, Broad-tailed Hummingbird *(Selasphorus platycercus)*, Western Wood Pewee *(Contopus sordidulus)*, White-crowned Sparrow *(Zonotrichia leucophrys)*, and Tree Swallow *(Iridoprocne bicolor)* (table 9).

The House Wren *(Troglodytes aedon)* had a significant population response to the 100 series (table 9) but did not demonstrate a habitat preference between the two series (table 10). Three species, the Warbling Vireo *(Vireo gilvus)*, Black-headed Grosbeak *(Pheucticus melanocephalus)*, and Mountain Bluebird, demonstrated a preference for the 100 series. Ten species showed a preference for the 200 series and four other species: Steller's Jay *(Cyanocitta stelleri)*; Clark's Nutcracker; Williamson's Sapsucker; and Pine Grosbeak, had densities too low to be statistically significant but were indicative of coniferous forest (table 10).

Correlation of Avifaunal and Vegetational Similarities

In addition to following specific differences and similarities in populations between stands and series it was possible to evaluate the

TABLE 10. Population responses of selected bird species to the overstory composition of the stand series.

Species	Stand series[a] $\bar{X}$ 100 (aspen)	Stand series[a] $\bar{X}$ 200 (conifer)	F-ratio$_{15\ d.f.}$
Turdus migratorius	9.1	8.8	NS
Dendroica coronata	6.0	6.3	NS
Junco caniceps	7.4	8.2	NS
Selasphorus platycercus	3.4	3.6	NS
Troglodytes aedon	8.3	4.6	5.7*
Spinus pinus	3.3	<u>9.6</u>	10.9**
Vireo gilvus[b]	<u>7.9</u>	3.2	15.5**
Contopus sordidulus[b]	4.1	3.6	NS
Zonotrichia leucophrys[b]	14.1	6.6	NS
Iridoprocne bicolor[b]	7.4	3.4	NS
Parus atricapillus	0.6	<u>4.2</u>	13.8**
Piranga ludoviciana	0.9	<u>3.2</u>	12.6**
Regulus calendula	0.0	<u>4.7</u>	27.3***
Catharus ustulatus	0.3	<u>1.6</u>	6.5*
Catharus guttatus	0.0	<u>2.6</u>	35.2***
Pheucticus melanocephalus	<u>2.0</u>	0.3	38.3***
Parus gambeli	0.0	<u>2.9</u>	6.3*
Spizella passerina	0.1	1.7	7.6*
Regulus satrapa	0.0	2.4	8.6*
Sitta canadensis	0.0	1.3	5.4*
Sialia currucoides	<u>1.7</u>	0.0	5.2*
Cyanocitta stelleri	0.0	0.4	NS
Nucifraga columbiana	0.0	0.4	NS
Sphyrapicus thyroideus	0.0	0.3	NS
Pinicola enucleator	0.0	0.2	NS

[a] $\bar{X}$ = mean of density indices; NS = not significant; * = $p < .05$; ** = $p < .01$; *** = $p < .001$; underlined = habitat preference shown.

[b] Recorded on all stands except 210, ES-SAF/Vaccae.

total avifaunal and vegetational similarities between the stands through the use of the similarity coefficient C = *2w/(a+b)*.

The similarity coefficients based on the composition and density indices for the bird species (table 11) were larger when pure aspen stands were compared to other 100 series stands ($\bar{x}$ similarity = 66.76%) and when stands containing conifers were compared to other 200 series stand ($\bar{x}$ = 63.98%) than in comparisons between the two series ($\bar{x}$ = 54.76%). The highest avian similarities were between stands 201 and 202 (81.6%) and stands 201 and 204 (81.7%). The three stands were composed of subalpine fir and quaking aspen. Stands 202 and 204 were both QA-SAF/Rudocc communities whereas stand 201 was a SAF-QA/Ribmon community (table 2). The avian similarity between stands 201 and 214 (both SAF-QA/Ribmon), however, was lower (58.7%) as was the similarity between stands 202 and 204, 70.5% (both QA-SAF/Rudocc). Thus, stands of the same plant community types did not show the greatest avian similarities. The stand with the lowest similarity coefficients with all other stands was 210 which had an Engelmann spruce-subalpine fir overstory ($\bar{x}$ = 33.5%). The mean similarity between 210 and the 100 series stands was 37.57% as compared to the mean similarity of 54.91% between 210 and the other 200 series stands.

The similarity coefficients based on the percent cover for the understory plants and the density by DBH size class for the tree species showed a similar relationship among the stands (table 11). The similarity coefficients were larger for comparisons within the 100 series ($\bar{x}$ = 30.73%) and within the 200 series ($\bar{x}$ = 36.08%) than between the two series ($\bar{x}$ = 22.07%). Again stand 210 had the lowest average similarity ($\bar{x}$ = 03.17%). The highest vegetational similarity, 82.5%, was

TABLE 11. Similarity indices for bird and plant species[a]. Indices of stands within the same community types are outlined.

	QA/ Symore	QA/Elygla		QA/Rudocc			QA/ Bromus	QA/ Ribmon	QA-SAF/ Rudocc		QA-SAF/ Symore	SAF-QA/ Ribmon-Symore	SAF-QA/ Ribmon		ES-SAF-QA/ Ribmon	ES-SAF/ Vaccae
Stand	105	111	112	103	108	116	109	215	202	204	207	206	201	214	213	210
105	--	.158	.528	.310	.430	.454	.391	.277	.520	.410	.390	.406	.223	.276	.123	.006
111	*.679*	--	.219	.069	.151	.192	.143	.073	.114	.055	.190	.083	.078	.088	.063	.006
112	*.760*	*.701*	--	.244	.375	.353	.292	.241	.431	.432	.415	.289	.145	.272	.130	.009
103	*.667*	*.620*	*.670*	--	.212	.361	.430	.280	.372	.442	.186	.216	.229	.289	.189	.006
108	*.691*	*.617*	*.650*	*.497*	--	.505	.293	.201	.381	.348	.380	.268	.152	.325	.089	.006
116	*.721*	*.627*	*.714*	*.554*	*.743*	--	.345	.279	.448	.825	.339	.296	.170	.396	.104	.006
109	*.766*	*.709*	*.714*	*.610*	*.640*	*.670*	--	.338	.286	.396	.303	.273	.245	.255	.176	.005
215	*.722*	*.633*	*.706*	*.552*	*.656*	*.779*	*.674*	--	.296	.403	.473	.321	.283	.453	.239	.015
202	*.624*	*.678*	*.679*	*.616*	*.508*	*.561*	*.623*	*.598*	--	.588	.498	.319	.378	.438	.154	.017
204	*.578*	*.638*	*.549*	*.506*	*.533*	*.523*	*.581*	*.565*	*.705*	--	.501	.403	.424	.377	.157	.019
207	*.620*	*.552*	*.577*	*.490*	*.545*	*.598*	*.629*	*.733*	*.657*	*.713*	--	.478	.326	.368	.170	.024
206	*.577*	*.576*	*.561*	*.473*	*.493*	*.560*	*.588*	*.690*	*.647*	*.755*	*.783*	--	.377	.425	.315	.100
201	*.615*	*.637*	*.636*	*.598*	*.476*	*.531*	*.656*	*.580*	*.816*	*.817*	*.686*	*.728*	--	.324	.206	.181
214	*.586*	*.533*	*.619*	*.457*	*.537*	*.615*	*.569*	*.667*	*.604*	*.594*	*.673*	*.664*	*.587*	--	.288	.032
213	*.449*	*.416*	*.453*	*.359*	*.404*	*.447*	*.468*	*.574*	*.524*	*.622*	*.670*	*.717*	*.569*	*.705*	--	.044
210	*.371*	*.453*	*.371*	*.303*	*.420*	*.387*	*.379*	*.456*	*.537*	*.597*	*.713*	*.516*	*.538*	*.511*	*.525*	--

[a]Indices for birds in italics.

between stands 116 (QA/Rudocc) and 204 (QA-SAF/Rudocc). The avian similarity for the same two stands was 52.3%.

Stands of the same community types did not have the greatest similarities for birds or for plants (table 11). In general the avian similarities ($\bar{x}$ = 59.63%) were higher than the vegetational similarities ($\bar{x}$ = 26.56%) between the stands. Only 5% of the stand comparisons for vegetational characteristics yielded similarities of greater than 50%, whereas 82.5% of the avian comparisons were above 50%.

A significant correlation was found between the vegetational similarities and the corresponding avian similarities for all the stands (F-ratio = 49.316, $p < .001$, 119 d.f.).

When the coefficients were utilized for only those stands on which conifers were present the correlation of similarities for birds and plants was again significant (F-ratio = 36.497, $p < .001$, 35 d.f.). However, a given degree of similarity in the vegetation of the aspen stands was not associated with a similarity based on the composition and density indices of the bird populations (F-ratio = 4.045, NS, 20 d.f.).

The only aspen stands with an avian similarity of less than 50% between them were 108 and 103, both QA/Rudocc communities. These stands had a vegetational similarity of 21% (table 11), and differed in tree size and spacing (density). The diameter distribution curve for stand 108 (fig. 4) approximated a normal probability curve around the fourth size class (10 cm) thus indicating an even-aged distribution. Increment cores revealed the age to be about 40 years. The trees forming the "tail" around the tenth size class (25.4 cm) were about 100 years old and probably were remnants of an earlier stand. Aspen of stand 103

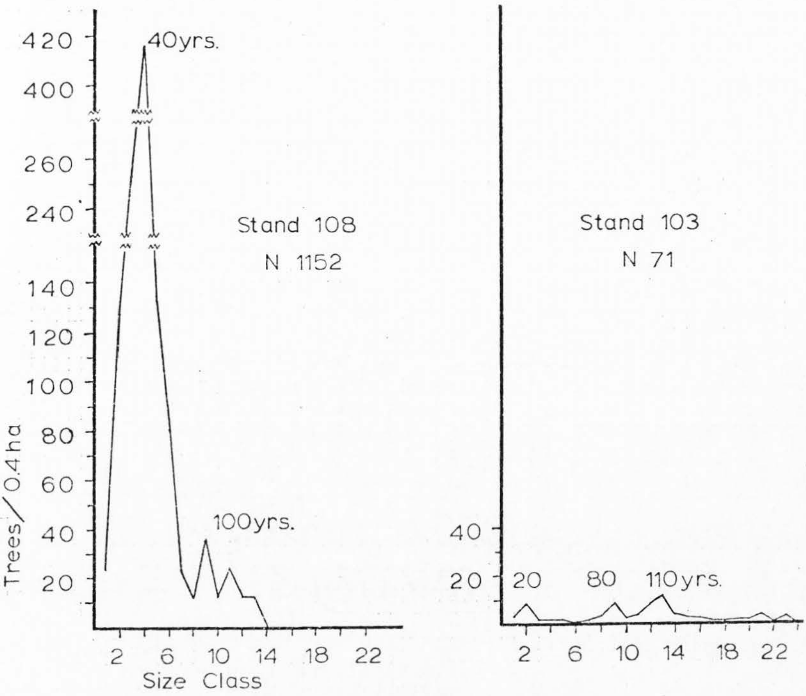

FIGURE 4. Comparison of diameter distributions in aspen stands 108 and 103.

(fig. 4) exhibited uneven-aged characteristics with peaks at ages 20, 80, and 110 years.

Stand 108 was very dense with 1152 trees per 0.4 ha and had 60% overstory coverage. The lush understory of *Sambucus* and *Rudbeckia* averaged 1 to 1.5 m in height. Bare trunks reached to an average of 6 to 8 m with very few dead branches immediately below the canopy. The 40-year growth which dominated the stand had a maximum height of 15 m and canopy depth of 7 m. The canopy of the few larger trees also started at about 8 m and reached to 18 m. Thus the major peak at size class 4 (10 cm) of the diameter distribution (fig. 4) accounted for most of the overstory. In contrast, stand 103 was very open with only 71 trees per 0.4 ha, 23% canopy coverage, and rather sparse ground cover. The canopy of the 80-year-old trees spanned from 2.5 m to 11 m and that of the larger trees reached from 3.5 m to 16 m. Thus the structure of the two stands was quite different.

Avian species with density indices in stand 103 at least twice as great as in stand 108 or present in 103 and absent in 108 were: House Wren *(Troglodytes aedon)*, Western Wood Pewee, Tree Swallow, Yellow-bellied Sapsucker *(Sphyrapicus varius)*, Common (Red-shafted) Flicker *(Colaptes auratus)*, Great Horned Owl *(Bubo virginianus)*, Hairy Woodpecker *(Dendrocopos villosus)*, Purple Martin *(Progne subis)*, Mountain Bluebird, Violet-green Swallow, and Swainson's Hawk. Species twice as abundant in 108 or absent in 103 were Audubon's Warbler, White-crowned Sparrow *(Zonotrichia leucophrys)*, Lazuli Bunting *(Passerina amoena)*, and Song Sparrow *(Melospiza melodia)*.

Diversity Indices and Forest Heterogeneity

Bird species diversity can be adequately described by counting the number of species present (Tramer 1969). In this study bird species diversity was significantly correlated with the total number of bird species utilizing the stand ($r = .902$, $p < .001$, 15 d.f.). Because bird species diversity was not more similar within plant community types than between types (table 7), other vegetational attributes besides the defined plant association were measured.

Correlation methods were used to evaluate the degree to which the measured vegetational characteristics and bird species diversity were related (table 12). The highest positive correlations with bird species diversity (BSD) included DBH diversity (DBHD), distance diversity by tree species (DD), and maximum DBH of fir. Variables negatively correlated with BSD were number of aspen per 0.4 ha, total foliage volume (TFV), and number of trees per 0.4 ha. Foliage volume diversity (FVD) was significantly correlated with BSD whereas foliage height diversity (FHD) and plant species diversity (PSD) were not significantly correlated with BSD. The age of the oldest tree sampled on each macroplot and BSD also were not significantly correlated ($r = .263$, $p > .1$, 15 d.f.). The highest positive association among the vegetation variables was between DBHD and DD ($r = .930$). These two variables had highly significant negative correlations with the number of aspen per hectare, and positive correlations with maximum DBH and maximum DBH of fir.

There were significant correlations between BSD and DBHD and the abundance of bird species and individuals (table 13). Additional correlations between BSD and distance diversities, tree numbers, and tree diversity also were significant (table 13). The correlation coefficient

TABLE 12. Matrix of correlation coefficients between Bird Species Diversity and vegetational characteristics.[a]

Variables[b]	BSD	Max. DBH	Max. DBH Aspen	Max. DBH Fir	Max. DBH Spruce	Aspen/ 0.4 ha	Fir/ 0.4 ha	Spruce/ 0.4 ha	Trees/ 0.4 ha	FVD	FHD	TFV	DD	PSD	DBHD
BSD	1.000	0.671[2]	0.276	0.794[3]	0.247	-0.709[2]	0.512[1]	0.015	-0.610[2]	0.555[1]	0.052	-0.623[2]	0.797[3]	0.297	0.853[3]
Max. DBH		1.000	0.658[2]	0.813[3]	0.263	-0.564[1]	0.176	-0.380	-0.712[2]	0.235	0.399	-0.289	0.814[3]	0.475	0.859[3]
Max. DBH Aspen			1.000	0.293	-0.184	-0.266	-0.412	-0.702[2]	-0.679[2]	0.034	0.664[2]	0.116	0.471	0.347	0.419
Max. DBH Fir				1.000	0.226	-0.476	0.524[1]	-0.074	-0.409	0.327	0.080	-0.559[1]	0.715[2]	0.442	0.848[3]
Max. DBH Spruce					1.000	-0.253	0.141	0.288	-0.096	0.179	-0.218	-0.248	0.441	-0.108	0.443
Aspen/ 0.4 ha						1.000	-0.451	-0.240	0.820[3]	-0.631[2]	0.150	0.496[1]	-0.779[3]	0.098	-0.746[3]
Fir/0.4 ha							1.000	0.579[1]	0.017	0.142	-0.512[1]	-0.407	0.264	-0.061	0.432
Spruce/ 0.4 ha								1.000	0.336	0.135	-0.978[3]	-0.225	-0.171	-0.485[1]	-0.060
Trees/ 0.4 ha									1.000	-0.560[1]	-0.404	0.321	-0.823[3]	-0.135	-0.701[2]
FVD										1.000	-0.027	-0.778[3]	0.560[1]	-0.139	0.422
FHD											1.000	0.177	0.245	0.424	0.104
TFV												1.000	-0.512[1]	-0.091	-0.522[1]
DD													1.000	0.180	0.930[3]
PSD														1.000	0.293
DBHD															1.000

[a]significance level: 1 = $p < .05$; 2 = $p < .01$; 3 = $p < .001$.

[b]BSD = Bird Species Diversity; FVD = foliage volume diversity; FHD = foliage height diversity; TFV = total foliage volume; DD = distance diversity; PSD = plant species diversity, DBHD = DBH diversity.

TABLE 13. Correlations between bird census values and vegetational characteristics.

Independent variables	Correlation coefficient $(r)_{15d.f.}$ BSD[a]	DBHD[a]
Total no. bird species	.902***	.822***
Mean no. bird species/census	.918***	.847***
Mean no. bird species/census stop	.828***	.791***
Mean no. bird individuals/census stop	.538*	.563*
DBH diversity (tree species)	.853***	
DBH diversity (tree type[b])	.838***	
DBH diversity (all trees)	.812***	
Distance diversity (tree species)	.797***	.930***
Distance diversity (tree type[b])	.774***	
Distance diversity (all trees)	.662*	
Total number tree species	.753***	
Total number tree types	.799***	
Tree species diversity	.754***	

[a]Dependent variable; * = $p < .05$; *** = $p < .001$

[b]Aspen or conifer

for BSD and DBHD was highest when the DBH's were sorted by tree species. Correlation coefficients for BSD and DD also were higher when the distances from center-points were recorded by tree species.

Bird species diversity indices were tested for significant differences between stands by the method of Hutcheson (1970). The same test was made for DBH diversity indices between stands. The levels of significance found between stands are given in table 14. A significant difference in BSD was found for 15.83% of the comparisons. No significant differences were found for comparisons of stands within the same community type or when stands within the same series were compared. The significant differences in BSD all involved comparisons of aspen stands (111, 108, and 116) to mixed aspen-conifer stands (204, 207, 206, 201, 214, 213, and 202). The DBHD comparisons produced somewhat different results. Significant differences were found in 65% of the comparisons. Fifty percent of the comparisons between stands within the same plant community types were significantly different. Of comparisons within the 100 series, 33.33% were significant as compared to 41.66% within the 200 series. However, 87.3% of the comparisons made between the two series were significant. There were thus greater differences in the DBH diversities when pure aspen stands were compared to stands containing conifers than in comparisons between stands of like tree composition.

Regression methods were used to determine the "best" functional relation among the vegetational characteristics and BSD. Multiple regression analysis showed that 97% of the variability in BSD for the 16 stands could be accounted for by the 14 measured vegetational characteristics given in table 15. The individual variable contributing the most to the mathematical function for predicting BSD ($\hat{Y}$):

TABLE 14. Significance levels of differences in Bird Species Diversity indices and DBH diversity indices[a]. Indices of stands within the same community types are outlined.

Stand	QA/ Symore	QA/Elygla		QA/Rudocc			QA/ Bromus	QA/ Ribmon	QA-SAF/ Rudocc		QA-SAF/ Symore	SAF-QA/ Ribmon-Symore	SAF-QA/ Ribmon		ES-SAF-QA/ Ribmon	ES-SAF/ Vaccae
	105	111	112	103	108	116	109	215	202	204	207	206	201	214	213	210
105	--	NS	NS	NS	NS	NS	NS	.01	.01	.01	.05	.01	.01	.01	.01	NS
111	*NS*	--	.01	.01	NS	.05	.05	.01	.01	.01	.01	.01	.01	.01	.01	.01
112	*NS*	*NS*	--	NS	.05	NS	NS	.05	.01	.01	NS	.01	.01	.01	.01	NS
103	*NS*	*NS*	*NS*	--	.05	NS	NS	.01	.01	.01	NS	.01	.01	.01	.01	NS
108	*NS*	*NS*	*NS*	*NS*	--	.05	NS	.01	.01	.01	.01	.01	.01	.01	.01	.05
116	*NS*	*NS*	*NS*	*NS*	*NS*	--	NS	.05	.01	.01	NS	.01	.01	.01	.01	NS
109	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	--	.01	.01	.01	.05	.01	.01	.01	.01	NS
215	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	--	NS	NS	NS	NS	NS	NS	.01	.05
202	*NS*	*NS*	*NS*	*NS*	*.05*	*NS*	*NS*	*NS*	--	NS	NS	NS	NS	NS	.01	.01
204	*NS*	*.05*	*NS*	*NS*	*.05*	*.05*	*NS*	*NS*	*NS*	--	.05	NS	NS	NS	.01	.01
207	*NS*	*.05*	*NS*	*NS*	*.05*	*.05*	*NS*	*NS*	*NS*	*NS*	--	NS	NS	.05	.01	NS
206	*NS*	*.05*	*NS*	*NS*	*.05*	*.05*	*NS*	*NS*	*NS*	*NS*	*NS*	--	NS	NS	.01	.01
201	*NS*	*.05*	*NS*	*NS*	*.01*	*.05*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	--	NS	.01	.01
214	*NS*	*.05*	*NS*	*NS*	*.01*	*.05*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	--	.01	.01
213	*NS*	*.05*	*NS*	*NS*	*.05*	*.05*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	--	.01
210	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	--

[a]Bird Species Diversity indices in italics.

TABLE 15. Functional relation among the vegetation variables and Bird Species Diversity[a]. Independent variables are progressively deleted by increasing individual contribution to the prediction of Bird Species Diversity (multiple regression analysis).

Independent variables		r^2 value
14 vegetational characteristics	(14 var.)	.97
X_5 Maximum spruce DBH deleted	(13 var.)	.97
X_4 Maximum fir DBH deleted	(12 var.)	.97
X_{13} Distance to tree species diversity deleted	(11 var.)	.95
X_3 Maximum aspen DBH deleted	(10 var.)	.94
X_{11} Foliage height diversity deleted	(9 var.)	.91
X_{12} Total foliage volume deleted	(8 var.)	.90
X_{14} Plant species diversity deleted	(7 var.)	.87
X_2 Maximum DBH (any tree species) deleted	(6 var.)	.84
X_7 Number fir trees/0.4 ha deleted	(5 var.)	.83
X_8 Number spruce trees/0.4 ha deleted	(4 var.)	.78
X_6 Number aspen trees/0.4 ha deleted	(3 var.)	.78
X_9 Number trees (all species)/0.4 ha deleted	(2 var.)	.78
X_{15} DBH diversity (individual remaining variable)		.73[b]

[a]Dependent variable

[b]F-ratio = 37.436, $p < .001$, 15 d.f.

$\hat{Y} = 1.97 - .0377X_2 - .0215X_3 + .00383X_4 - .00349X_5 - .0407X_6 - .0386X_7 - .0464X_8 + .0405X_9 + .1375X_{10} - 2.3786X_{11} + .0000371X_{12} + .258X_{13} + .3857X_{14} + .5427X_{15}$ was DBHD, X_{15} (table 15).

BSD was significantly correlated with DBHD ($r = .8531$, $p < .001$, 15 d.f.) and regression analysis yielded a line with a slope of .372 (fig. 5).

The differences in structure between some of the aspen stands could be seen by comparing the diameter distributions of the trees (fig. 6). Stand 111 was composed of many uniform small diameter trees about 80 years old, and a few larger ones 115 years in age. The diameter distribution was approximately bimodal with a major peak at size classes 5 and 6 (13-15 cm) and a secondary peak at size classes 9 and 10 (23-25 cm). There were 832 trees per 0.4 ha with 80% overstory coverage. The stand had 59% ground cover dominated by *Lathyrus* and graminoids (table 4). Many aspen root suckers (167 per 50 m^2) were growing under the dense overtopping canopy. The largest of the suckers reached a height of approximately 2 m and had a DBH of 2 cm. However they produced a very sparse lower story in the dense stand of bare trunks which reached to 11 m before the canopy began. The total height of the canopy was about 15 m. The larger, 115-year-old trees, represented by the secondary peak in the diameter distribution curve (fig. 6), did not produce a visibly separate layer in the canopy. This stand had a low DBHD of 1.804.

An increase of DBHD (2.290) was found in stand 105 which had more size classes of trees and a smaller proportion of the total in the most represented size class. The primary peak was at size class 3 (8 cm) which was made up of 50-year-old trees. The remainder of the diameter

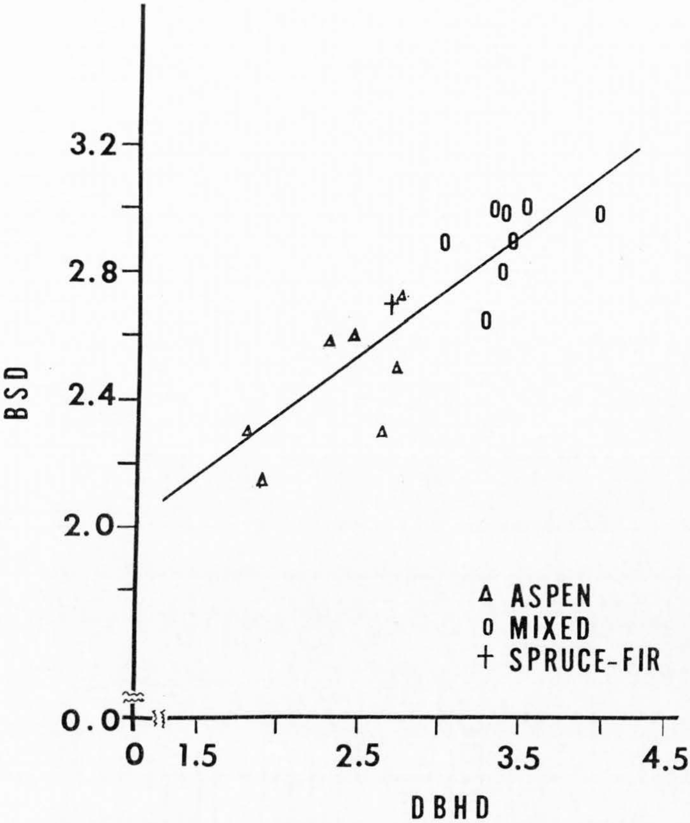

FIGURE 5. Index of heterogeneity (DBHD) and bird species diversity (BSD) for aspen, mixed aspen-conifer, and spruce-fir communities of the Wasatch Plateau in central Utah ($r = .853$, $p < .001$, 15 d.f.).

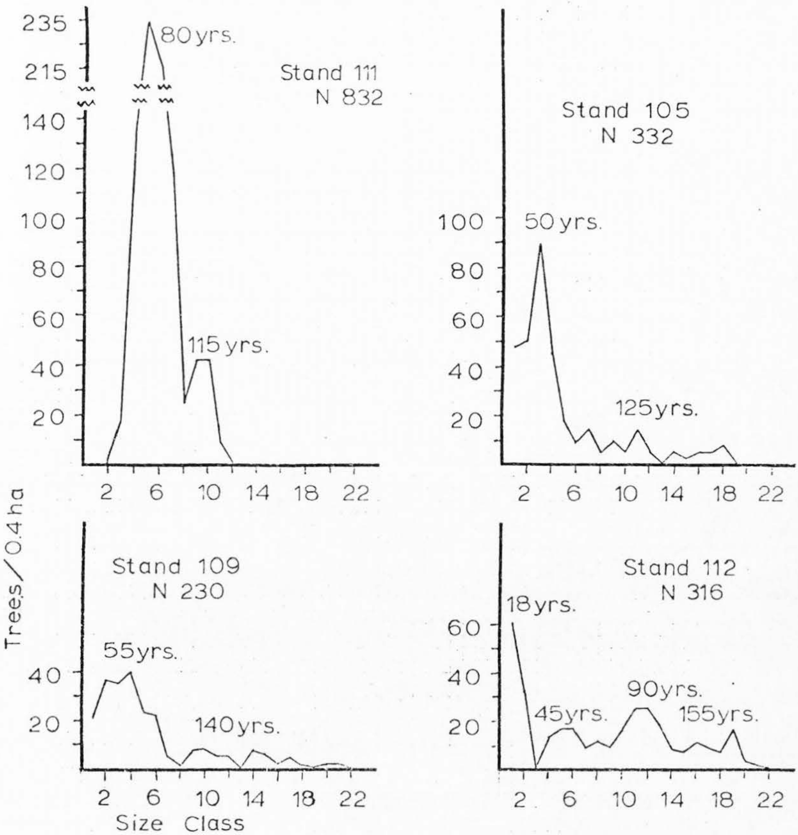

FIGURE 6. Comparison of diameter distributions in four aspen stands.

distribution was uneven-aged with no significant peaks (fig. 6). The trees of the predominant size class comprised a low level of the canopy, spanning from 3 m to 8 or 9 m. The top of the abundant small trees met the bottom of the canopy of the larger trees. The canopy of the large trees reached to 18 m in height. The canopy of trees smaller than class 3 (7 cm) was continuous down to the ground cover plants. Thus all aspen over 1.35 m in height were part of the canopy cover which was made up of many layers.

DBHD was again higher in stand 109 (2.637) which had still a few more size classes and more equal distribution among the classes (fig. 6). The height to the top of the canopy of the larger, older trees was 20 m and the bottom of the canopy was at 5 m. The canopy of the 55-year-old growth started at 3 m and reached to 9 m. Canopies were continuous down to 2.4 m and a few extended down to 1.2 m. As in stand 105 there was no band of bare trunks without overlapping foliage. There were 230 trees per 0.4 ha with 55% canopy coverage.

The greatest DBHD (2.728) of the aspen stands occurred in stand 112 which had 60% canopy cover and 316 trees per 0.4 ha. The canopy of the large trees reached 25 m and was continuous down to 16 m. There were dead branches below the canopy down to 4 m. Canopies of the other size classes ranged from 3 m to 13 m, 2 m to 8 m, and 2 m to 3.5 m with dead branches down to 2 m for all size classes. The cover of the small trees extended down to 1 m. Stand 112 contained proportionately more trees of large DBH, and more equal distribution among the size classes than the other aspen stands. It also contained many dead branches in the lower half of the canopy. The peak in the diameter distribution curve (fig. 6) was part of the lower canopy rather than part of the overstory. A layer comprised of uniform, bare trunks standing like so many white pickets supporting the canopy as was found in stands 108 and 111 was not present in stand 112.

BSD increased across the aspen stands in the same order as did the DBHD, from a low in the uniform dense stands to a high in stand 112 which contained the tallest trees and had more layers in the canopy than the other stands.

The spruce-fir stand, 210, was a dense stand of uniformly small conifers with 731 trees per 0.4 ha and 85% canopy coverage. There was one Engelmann spruce with a DBH of 47 cm in the stand. An increment core showed that it took 150 years for the spruce to reach 15 cm in DBH and that it had grown 30 cm in the last 85 years. The stand had evidently been burned or cut in the 1890's and the remaining trees had been released. Most of the present overstory had started from seed at that time. Spruce dominated the overstory almost four to one over fir (fig. 7). However, there were 156 fir seedlings and only 5 spruce seedlings in the 50 m^2 sample. Fifty percent of the trees between 2 and 5 cm were dead; the living 2-5 cm trees reached about 6 m in height. Most of the larger trees were between 13 and 16 m tall with dead branches starting at 6 or 7 m and continuing to the ground.

The diameter distribution of the conifer stand 210 reflected a DBHD of 2.707, almost equal to that of aspen stand 112 (2.728). The BSD of 210 (2.731) also was comparable to that of stand 112 (2.750), the aspen stand with the highest diversity.

Stand 202 contained a mixture of the two life forms, deciduous and coniferous trees (fig. 8). There were 150 trees per 0.4 ha with 40% canopy coverage. The fir trees were beginning to overtake the aspen in

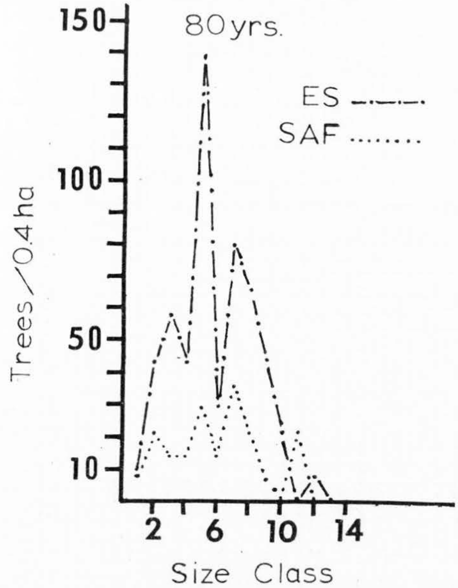

FIGURE 7. Diameter distribution in stand 210.

height; fir reached 20 m and aspen 15 m, and 8% of the aspen over 18 cm DBH were dead.

The DBHD of stand 202 (3.363) was greater than that of any single life form stand. The BSD (2.819) also was higher than in the single life form stands. The only mixed aspen-conifer stand which had a BSD lower than stands 210 and 112 was stand 215 which was an aspen community type with 70% aspen canopy coverage and only 5% fir coverage.

Stand 213 represented a high DBH diversity stand (3.977) with a reasonably even distribution of three tree species across many size classes (fig. 9). BSD was correspondingly high (2.958). The highest

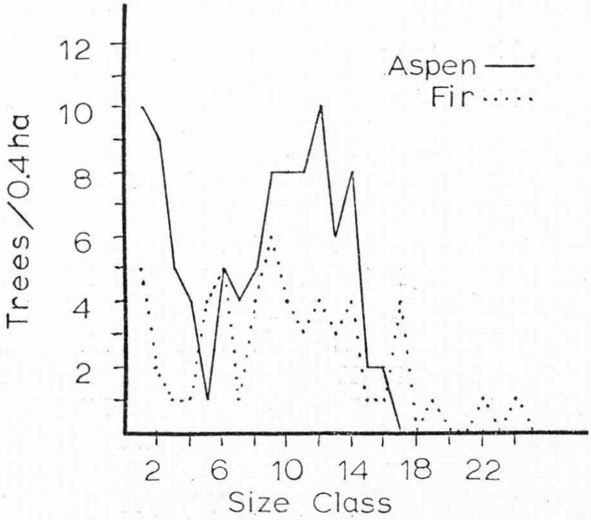

FIGURE 8. Diameter distribution in stand 202.

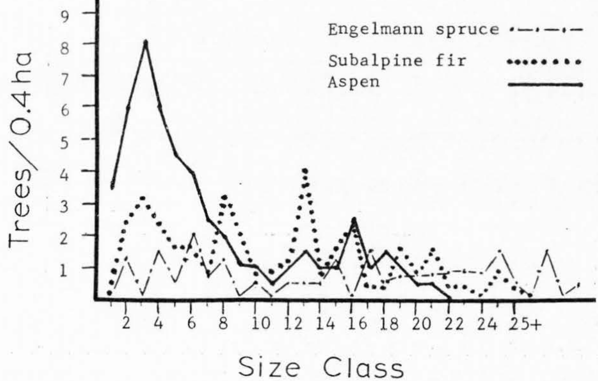

FIGURE 9. Diameter distribution in stand 213.

BSD (3.033) occurred in stand 214, also comprised of the three tree species.

Tree DBH was significantly correlated with tree height ($r = .896$, $p < .001$, 59 d.f.) and canopy radius ($r = .670$, $p < .001$, 59 d.f.) for a representative sample of trees on the 16 stands.

DISCUSSION

Vegetation Stands

The soil and climatic differences between the east- and west-facing slopes appeared to affect the plant species composition of both the overstory and understory. All stands with pure aspen overstories were on west-facing or northwest-facing slopes except the QA/Symore community, 105, which had an aspect of 60° NE. The aspen stands with *Elymus* and *Bromus* understories were all on west-facing slopes (table 2). The grasses were better adapted to the drier west-facing slopes than were the conifer seedlings which required more soil moisture (Jones 1974).

The QA/Rudocc communities are thought to reflect disturbances in the recent past (J. Henderson, pers. comm.). Grazing may have reduced the coverage of grasses on these stands as suggested by Baker (1925). Also, grazing may have had a direct effect through trampling or removal of conifer seedlings. It also was possible that small conifer seedlings had been killed by damping-off fungi when covered by dead plant material during the winter (Tappeiner and Helms 1971). Stands 108 and 116 had very lush herbaceous understories and may have thus prevented conifer establishment. Lack of moisture on the NW aspects did not appear to limit conifers directly in the QA/Rudocc communities because subalpine fir were established in stands 215, 204, and 207, which were also on northwest-facing slopes at similar elevations (table 2).

The other mixed aspen-conifer stands were on north- and northeast-facing slopes where more soil moisture was available (Jones 1974). Conifer seedlings were more abundant in stands on north-facing slopes than on any other exposure. The highest concentration of conifer seedlings was found in stand 210 which lacked both aspen and lush ground cover. Thus soil and climatic conditions dependent upon topographic aspect, grazing, and the presence of thick herbaceous cover and aspen all may have inhibited conifer seedling establishment at elevations greater than 2400 m on the Wasatch Plateau of Utah.

The shrubs present in the different plant communities did not produce a distinctive structural layer separate from the herbaceous cover. However, there was very little shrub cover in the QA/Elygla and QA/Bromus communities on the dry west-facing slopes (table 4). Shrubs usually were associated with *Rudbeckia* and other tall herbaceous cover.

The stands represented a range of structural variation found in aspen, aspen-fir, aspen-spruce-fir, and spruce-fir communities on the Wasatch Plateau. Stands of the same plant community types varied in tree size and spacing (density), and thus reflected different histories. This was especially evident for stands 108 and 103, both QA/Rudocc communities (fig. 4).

Plant communities are recognized by their gross structure or physiognomy as determined by the life forms of the dominant species and their spacing (Kendeigh 1974:27). In this study the life forms and spacing of plants appeared to be dependent upon the topographic aspect and resulting soil and climatic conditions as well as on grazing pressures and fire or logging histories of the stands.

The presence of large conifers and the low density of aspen in the 200 series stands significantly contributed to the habitat differences between the two series (table 8). However, there was not a significant difference in the size of aspen between the series. The size and spacing (density) of aspen did account for the habitat differences between stands of the 100 series. For stands 108 and 103, both QA/Rudocc communities, the differences in tree size and spacing were a result of different histories rather than climatic conditions because both were on northwest-facing slopes at approximately the same elevation (table 2).

Bird Species Richness

The number of bird species in each stand per year (table 5) corresponded to the findings of other studies. In a review of North American bird surveys Udvardy (1957) found most samples for deciduous forest contained 15 to 30 species with a range of 7 to 39 species. Twenty-six breeding species were recorded in the aspen parkland of central Canada by Bird (1930). Salt (1957) reported a total of 19 breeding species for aspen and 19 species for spruce-fir areas in Wyoming. In another study in the west, Tatschl (1967) in New Mexico reported 25 breeding species for aspen and nearly as many for spruce-fir communities. Young (1973) observed 25 breeding species and 20 visiting species in two aspen stands in northern Utah during two seasons. Flack (1976) listed a total of 27 breeding species for three aspen areas on the Wasatch Plateau of Utah. Winternitz (1976) found 24 common bird species in aspen-willow and 22 species in spruce-aspen vegetation on Colorado's Front Range. In the present study 50 species were recorded; 32 in aspen cover, 44 in mixed aspen-conifer cover, and 22 in spruce-fir (table 6).

Species abundance, as measured per census stop, per complete census, and the total number of species recorded for the two years (species richness), varied across the stands (table 7). The highest numbers of species occurred in the mixed aspen-conifer stands, with the exception of stand 215 which had only 5% conifer coverage (table 4).

Bird species richness was not more similar within plant community types than between community types. This suggested that some attributes of the vegetational configuration of the stands which were not designated by the community type classification were more important to the birds than the limits of the defined plant associations.

The significant differences in bird species richness and the mean numbers of birds per census between the 100 and 200 series (table 8) indicated that several different bird species were responding to the different tree compositions of the series. Abundance values were higher for stands containing a mixture of aspen and conifers than for either pure aspen or all conifer stands (table 7). The habitat requirements for two groups of bird species, those adapted to deciduous and those adapted to coniferous forests, were satisfied by the mixed aspen-conifer communities. Eighteen species were recorded only on stands of the 200 series and an additional 5 species had a significant population response to the 200 series (table 9). The lowest number of individuals per census stop was found in the conifer stand, 210. Salt (1957) and Tatschl (1967) also found very low numbers of individuals in spruce-fir as compared to aspen communities, although bird species richness was comparable between the plant communities.

Habitat Preferences

The bird species recorded in the aspen stands closely paralleled Flack's (1976) species list for his study areas on the Wasatch Plateau. Many of the species were the same as those found in aspen by Salt (1957) in Wyoming and by Winternitz (1976) in Colorado.

Structural features of aspen stands which are known to influence the density of some bird species are the density and DBH of the trees

(Hickey 1956, Flack 1976). Flack (1976) found that the number of woodpeckers increased when the average DBH of aspen was greater than 15 cm and there were between 100 and 300 trees per 0.4 ha. Flack also showed a correlation between the number of species or individual birds dependent upon cavities and the number of species of birds which excavated cavities in aspen. A similar association among cavity nesting species in aspen stands of northern Utah was observed by Young (1973). Winternitz (1976) found that in the aspen on her study site in Colorado only woodpecker holes were used by other cavity nesters. She concluded that the number of woodpeckers may in part determine the numbers of other species.

In this study several cavity nesting species had their highest densities (table 5) in stands 112, 103, 116, or 109 which contained large aspen trees (DBH up to 50 cm). These species included the House Wren, Common (Red-shafted) Flicker, Yellow-bellied Sapsucker, Tree Swallow, Mountain Bluebird, Purple Martin, and Violet-green Swallow. Yellow-bellied Sapsuckers, which nest most often in aspen (Bailey and Niedrach 1965), and Red-shafted Flickers appeared to account for the large number of nest cavities present in stand 103. In 1974 the nest of a Hairy Woodpecker also was found in the stand. The low number of trees per 0.4 ha in 103 (table 2) provided the open spaces necessary for the aerial feeding of the swallows and the Purple Martin. The Swainson's Hawk was found exclusively in this stand which was very open and had sparse ground cover.

None of the species exclusive to mixed aspen-conifer cover required both life forms but, rather, they were present simply because their requirements were satisfied by conifers, aspens, shrub cover, or nearness to water alone.

The MacGillivray's Warbler was found only in stands 202, 207, 214, and 213 (table 5) all of which had shrub dominated understories and small spring run-off streams. Anderson and Shugart (1974) found that the abundance of the Downy Woodpecker was correlated with the number of deciduous saplings. There were saplings present in both stands 201 and 214 in which the woodpecker was recorded. The Wilson's Warbler was exclusive to stands 215 and 214, both of which were in close proximity of Fairview Lake. These three species were not included as breeding birds of the climax coniferous forest by Snyder (1950). The species all appeared to be responding to environmental factors other than the composition of the overstory.

The Clark's Nutcracker, Blue Grouse, White-breasted Nuthatch, Williamson's Sapsucker, Brown Creeper, and Pine Grosbeak were classified by Snyder (1950) as breeding species of the climax coniferous forest. The White-breasted Nuthatch also was classified within a deciduous community by Anderson (1972). This species occurred only in stand 207, an aspen-dominated mixed community (table 4). The Blue Grouse, a ground nester, may have been responding to the ground cover as well as to the overstory composition but the sample size was too small to show any trends. The remaining four species exclusive to mixed cover, as well as the Steller's Jay (which was also recorded in the conifer stand) were all found in stands 213 and 214 which contained large fir trees (over 30 m in height) and some spruce coverage. These inhabitants of coniferous forest appeared to be responding to the coniferous life form present in the two stands.

The Ruffed Grouse is characteristic of several stages of both life forms rather than to coniferous forest alone (Pitelka 1941), and was probably responding to the structure of the understory of the conifer stand, 210. The Sharp-shinned Hawk, however, is known to be a coniferous forest species (Snyder 1950, Hagar 1960). A pair was nesting in the spruce-fir stand, 210, both seasons.

Specific differences in population levels between the stands and the series were more distinct for the common (high constancy) bird species. The 10 most common species also were the ones with the highest population densities across the range of stands (table 5). Of these the American Robin, Audubon's Warbler, Gray-headed Junco, and Broad-tailed Hummingbird did not demonstrate population differences among the series or stands.

The House Wren was found by Young (1973) in both brushy and open aspen stands in northern Utah, although it was more abundant in a stand of large trees where more nest cavities were available. In the present study the highest House Wren densities were in stand 112 and 103 which contained large aspens and were inhabited by other cavity nesters.

The Warbling Vireo is known to show a decided preference for aspen and cottonwoods (Bent 1950, Bailey and Neidrach 1965, Grinnell and Miller 1944, Winternitz 1976) and the Black-headed Grosbeak is usually found in deciduous trees and shrubs (Bent 1968). Both species demonstrated a habitat preference for the 100 series (table 10) and were absent in stand 210 which lacked aspen.

The Western Wood Pewee did not demonstrate a preference between the two series, although it was not recorded in stand 210 which lacked aspen (table 9). It also had low densities in stands 213 and 214 (table 5) which contained large fir trees, over 30 m tall, and some spruce coverage. Pewee density also was low in stand 108 which had a very high number of small aspen (fig. 4). This stand lacked the wide-open pattern of branchwork preferred as lookout perches and song posts by the pewee (Grinnell and Miller 1944, Flack 1976) and dead horizontal branches favored as nest sites (Bent 1942, Bailey and Niedrach 1965, Young 1973). The pewee was responding to the presence, structure, and spacing of the aspen in the stands.

The White-crowned Sparrow also did not have a significant mean population difference between the two series (table 10). The highest densities for this species occurred in stands 108 and 116 which had lush, shrubby ground cover. White-crowned Sparrows were absent in stand 210 which had very little ground cover (table 2).

Ten species showed a preference for the 200 series. All of these were classified as coniferous forest species by Hayward (1945), Snyder (1950), and Kendeigh (1974). The Chipping Sparrow *(Spizella passerina)* was not present in stand 210 and occurred in stands with fewer than 300 trees per 0.4 ha and with generally low ground cover percentages. It appeared to be responding more to the structure of the understory than to the composition of the overstory. The Western Tanager *(Piranga ludoviciana)* had consistently higher densities in stand 214 but did not demonstrate any other discernable population trends.

The Hermit Thrush *(Catharus guttatus)* and Swainson's Thrush *(Catharus ustulatus)*, both low shrub-nesters, had population densities too low to demonstrate any responses to the understory. The Lazuli Bunting *(Passerina amoena)*, not characteristic of either series (table 9), did demonstrate a response to the shrub understory. It was more than twice as abundant in stand 215, which had a total shrub coverage of 59%, than in any other stand (table 5).

The Ruby-crowned Kinglet *(Regulus calendula)*,Mountain Chickadee *(Parus gambeli)*, Golden-crowned Kinglet *(Regulus satrapa)*, and Red-breasted Nuthatch *(Sitta canadensis)* were all exclusive to the 200 series whereas the Pine Siskin *(Spinus pinus)*, Black-capped Chickadee *(Parus atricapillus)*, Chipping Sparrow, and Western Tanager occurred in both series. Anderson (1972) classified the Black-capped Chickadee with a deciduous community and the Red-breasted Nuthatch with a coniferous community. In the present study the Black-capped Chickadee had its highest population densities in mixed stands with high coniferous composition (213) and in the conifer stand (210).

Correlation of Avifaunal and Vegetational Similarities

The avifaunal similarity coefficients were largest for comparisons between stand of the same series (table 11). This reflected the importance of the life forms. Several bird species showed a significant population response to the overstory composition of the series (table 9). The lowest similarity coefficients were between stand 210, which had an Engelmann spruce-subalpine fir overstory, and the pure aspen stands. The avian similarities became lower as the differences in the tree cover types between the stands became greater. The Black-capped Chickadee, which was more abundant in the mixed aspen-conifer and spruce-fir stands than in the aspen stands, and the other coniferous forest birds exclusive to the 200 series were responsible for this difference in avian similarity among the cover types. The important contributing species included the Ruby-crowned Kinglet, Hermit Thrush, Mountain Chickadee, Golden-crowned Kinglet, Red-breasted Nuthatch, and Steller's Jay.

The fact that stands within the same plant community types did not show the highest avian similarities indicated that the vegetational measure of stand similarity was not of a scale important to the bird species. The coefficients of similarity, based on the percent cover for the understory species and the density by size class for the tree species, reflected to a greater degree the understory species composition than they did the structure of the overstory. The plant species composition of the understory appeared not to be as important to most bird species as was the composition and structure of the overstory.

The similarity coefficients between stands based on the composition and density indices of the bird populations utilizing those stands were higher than the similarity coefficients based on the vegetational characteristics of the stands. This was because the majority of the breeding habitats of the birds did not coincide with the well-defined, restricted plant associations. Oelke (1966) summarized the same relationship with habitat for European birds.

Different plant species provided for the needs of many of the bird species. This was especially evident for the common birds which showed no population trends among the stands. These included the American Robin, Audubon's Warbler, Gray-headed Junco, and Broad-tailed Hummingbird. Requirements of a particular structural feature such as brush cover also were met by different plant species providing the same structure. For example the Lazuli Bunting responded to *Symphoricarpos*, *Ribes*, and *Sambucus* alone and in different combinations as suitable brush cover. The plant species composition of neither the overstory nor the understory appeared to be of great importance to the White-crowned Sparrow as long as there was a high percentage of ground cover. Thus the structure of the plant community rather than its taxonomic composition was of importance to the inhabiting birds.

Correlations were made to determine if a given degree of vegetational similarity between two stands was associated with a similarity in the composition and densities of the corresponding bird populations. A given degree of similarity in the vegetation of the stands within the 100 series was not correlated with the corresponding avian similarity. However, a significant correlation was found between the similarity of the vegetational parameters and the avian characteristics for the 200 series stands. The distribution and structure of the important vegetational characteristics which determined the composition and density of the bird species were more similar among the mixed stands than between the aspen stands. This was because the mixed stands did not demonstrate the extremes in DBH distribution and tree spacing that existed between the aspen stands. The mixed stands all contained aspen of large DBH, and had many represented size classes with fairly even distribution of trees among the classes.

The extremes in the structural composition of two aspen stands of the same community type were especially evident for stands 108 and 103. The tree DBH distributions were very different for the two stands. Stand 108 was comprised of uniformly sized, approximately 40-year-old trees whereas stand 103 was unevenly aged (fig. 4). There was thus greater diversity in tree size and spacing in stand 103. Both stands were QA/Rudocc communities, and both were on northwest facing slopes at approximately 2675 m. The stands were separated by a distance of about 8 km. They also differed in percent understory cover; stand 108 had very lush ground cover as compared to only 53% in 103 (table 2). Stands 103 and 108 were the only aspen stands with an avian similarity of less than 50% between them. Eleven of the 15 bird species responsible for this low avian similarity coefficient were more abundant in stand 103 than in 108. Of these, eight were cavity nesters and were dependent upon the large DBH of the trees. Four of the cavity nesters, the Tree Swallow, Purple Martin, Violet-green Swallow, and Mountain Bluebird, fed on insects in flight and foraged in open areas. The other three species, the Western Wood Pewee, Great Horned Owl *(Bubo virginianus)*, and Swainson's Hawk, also foraged in open areas. The other four species, more abundant in stand 108 than in 103, were the Audubon's Warbler, White-crowned Sparrow, Lazuli Bunting, and Song Sparrow. The Audubon's Warbler, a canopy foraging species in aspens (Young 1973), was responding to the high foliage volume in stand 108. The other three species were ground- and low shrub-nesters and were responding to the lush understory. Thus the nesting and foraging requirements of the bird species present were met by the structure of the stands.

Diversity Indices and Forest Heterogeneity

It has been well documented that as the structural complexity of the vegetational component of the habitat increases, the number of bird species increases (MacArthur and MacArthur 1961, MacArthur, Recher, and Cody 1966, Karr 1968 and 1971, Recher 1969, Karr and Roth 1971, Willson 1974, Roth 1976, and others). However, the biological meanings underlying the methods and measures used to predict bird species diversity are not as well understood (Willson 1974).

According to Tramer (1969:928) bird species diversity during the breeding season can be described adequately by the numbers of species present because "the factors which regulate bird species diversity do so by determining the number of species which can coexist in a given habitat." An increase in structural variability in three dimensions leads to an increase in avian species through the exploitation of more available, discernible space (Willson 1974, Roth 1976). Therefore a measure of the spatial variability in the vegetational configuration of the habitat should provide an index to the number of bird species utilizing the habitat.

In this study the habitat features which appeared to have ecological relevance to most of the bird species were the size, spacing, and life form of the trees. Fourteen features which appeared to contribute to environmental patchiness (spatial variability in the vegetational configuration) were measured and tested for a relationship with BSD (table 12). Nine of the vegetational characteristics were significantly correlated with BSD.

Plant species diversity and the vertical measure of foliage height diversity were not predictive of BSD in this study. These parameters did not measure horizontal patchiness, an important component of forest heterogeneity (Roth 1976).

The highest correlation among the vegetational variables was for DBHD and DD (table 12). Aspen stands usually decrease in tree density and increase in tree DBH as they mature; these changes are accompanied by altered bird species composition (Flack 1976). The number of species comprising the coniferous forest avifauna also is lower in uniform stands of small trees (Udvardy 1957). In this study fifteen bird species were found to have population responses to the differences in size and density of trees between aspen stands 103 and 108.

DBHD and DD were highly correlated with BSD (table 13). The DBH and distance variables were more highly correlated with BSD when the values were sorted by tree species. indicating again a response by the bird species to the life forms. The correlation of BSD with the number of life forms present was higher than with the total number of tree species or tree species diversity in the stands (table 13). This was evident in the stand data because, although BSD was highest in stands in which all three tree species were present (aspen, spruce, and fir), BSD was higher in stands having both life forms (deciduous and coniferous) than in stand 210 which had only the two coniferous species (table 7).

Significant differences in BSD indices were found when some of the aspen stands were compared to the mixed aspen-conifer stands (table 14). This reflected the low species richness of aspen stands 111, 108, and 116 as compared to the high species richness of the mixed aspen-conifer stands (table 7). Winternitz (1976) also found high species richness in spruce-aspen vegetation. The habitat requirements of more bird species were met by the presence of both the deciduous and coniferous life forms in the mixed stands. Tramer (1969) also found higher BSD in mixed hardwood-coniferous forests than in either coniferous or deciduous forests.

The DBH diversity indices usually were significant when stands with a different number of tree species were compared. This was because more size classes were represented when more tree species were present. The number of size classes present varied according to the different histories of the stands.

Multiple regression analysis showed that 97% of the variability in BSD for the 16 stands could be accounted for by the 14 measured variables (table 15). Other variables such as the presence of water (MacArthur 1964, Karr 1968) and/or the percent ground and shrub cover appeared to be more important to some species such as the MacGillivray's Warbler, Wilson's Warbler, Yellow Warbler *(Dendroica petechia)*, Song Sparrow, White-crowned Sparrow, Chipping Sparrow, Lazuli Bunting, and Ruffed

Grouse than the composition and structure of the overstory. These variables as well as the bird species composition of the stands may have accounted for the rest of the variability in BSD.

The individual variable contributing the most to the mathematical function for predicting $\hat{Y}$ (BSD) on the basis of the overstory structure and plant species composition of the stands was DBHD. BSD was significantly correlated with DBHD and regression analysis yielded a line with a slope of .372 (fig. 5). This index was tested by correlation coefficient because it is not itself a controlling factor but an expression of many competitive and other environmental factors controlling the variation in tree height and shape considered the major cause of heterogeneity in forests.

What was the biological meaning of this vegetational correlate to bird species diversity? DBHD was highly correlated with distance diversity as derived from the point-centered technique. The distances gave information about dispersion and density and therefore should have measured horizontal heterogeneity. Tree DBH was significantly correlated with tree height and canopy radius at its greatest point, constituting therefore an indirect measure of vertical heterogeneity. DBHD therefore was a measure of both the vertical and horizontal components of the habitat. Since the DBH values were sorted by tree species, DBHD also was a measure of the variability in life form. Variations in the size, spacing, and life form of trees should create patches of different densities and configurations and, consequently, patches detected and responded to by several different bird species. The increased environmental patchiness in three dimensions, leading to new possibilities of differential space exploitation, would allow more bird species to be packed into the area (Willson 1974, Roth 1976).

The diameter distribution of aspens per 0.4 ha for stand 111 represented a low DBHD with an uneven distribution of one tree species across few size classes (fig. 6). BSD and bird species richness also were low indicating few bird species were able to partition the habitat spatially because there were few discernable patches. Roth (1976) also found that closed-canopy forests supported a lower BSD than forests with broken canopies. As the number of size classes represented in the aspen stands increased and the distribution of trees between the size classes became more equal (fig. 6), the BSD increased. The increased spatial heterogeneity in these stands with greater tree height and more layers in the canopy resulted in new possibilities of differential space exploitation and thus provided for more bird species. The mixed aspen-conifer stands exhibited a further increase in three dimensional patchiness with the presence of even larger trees and two life forms (figs. 8, 9). BSD again increased because bird species richness was higher in the mixed stands. Although some deciduous forest bird species dropped out with increased coniferous coverage, they were replaced by coniferous forest bird species.

CONCLUSIONS

The topographic aspect and resulting soil and climatic conditions of the stands appeared to be limiting factors in determining which life forms could potentially develop in a stand. The different histories of the stands accounted for the differences in establishment and spacing of the life forms present. Grazing pressures and length of time since the last major disturbance were considered to be of historical importance. The differences in topographic aspect and histories of the stands had an indirect effect on the bird populations through the resulting vegetational structures.

The habitats of the bird species were not restricted to the well-defined plant associations although several species did respond to the different life forms. Bird species richness was highest in the mixed aspen-conifer stands because the habitat requirements of both birds adapted to the deciduous life form and birds adapted to conifers were met in these stands.

There were some general population trends exhibited by the bird species to the range of stands. Some species responded to water and/or the structure of the understory rather than to the tree life forms. However, several species did show a population response to the structure and composition of the overstory. Within the aspen stands, cavity nesters and aerial feeders were more abundant in open stands containing trees of large DBH whereas some canopy foraging species were more abundant in dense stands. Species which favored the deciduous life form tended to decrease in abundance as the percent canopy coverage of conifers increased in the mixed stands, and they were not present when aspen were lacking. Coniferous forest species increased in abundance in those mixed stands with increased coniferous coverage. However, the conifer stand had low individual bird numbers because of its uniform structure.

The diversity of the distribution of tree species' DBH was found to be a predictive index of BSD. Uniform stands of small trees, all of the same life form, had both a low DBHD and a low BSD. Stands with more size classes represented, therefore containing larger trees and more equal distribution of the trees between the size classes, had higher DBHD and BSD than uniform stands. The highest DBHD and highest BSD were found in stands containing large trees of both life forms with many layers in their canopies.

DBHD was correlated with DD, a measure of tree dispersion and density or horizontal heterogeneity. It was also an indirect measure of vertical heterogeneity since tree DBH was correlated with tree height and canopy radius. DBHD also was a measure of the variability of life forms because the DBH values were sorted by tree species. DBHD was therefore an index of three dimensional environmental patchiness.

Increased environmental variation lead to new possibilities of differential space exploitation by more bird species since more patches could be detected and utilized. Johnston and Odum (1956:59) made similar conclusions in a successional study: "as plants increase in height, volume, and diversity of life form, the available niches increase". Oelke (1966) summarized the same pattern in European communities as the greater the number of layers in a habitat, the higher the avian density.

DBHD was a simpler and faster way to measure index of forest heterogeneity than FHD, FVD, and PSD, none of which predicted BSD in this study.

DBHD also was easily visualized by the variation in life forms and the number of stories within the stand.

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APPENDIX. Total species list by decreasing constancy giving average coverage % (all values < 1% coverage are recorded as .3). See text and Table 3 for species code names.

Species Code	Constancy (%)	Study stands															
		105	111	112	103	108	116	109	215	202	204	207	206	201	214	213	210
Lathyr	100	5	24	9	7	1	2	4	2	4	1	1	3	1	.3	4	1
Stejam	94	3	1	3	12	7	12	9	4	2	4	4	5	4	9	4	*
Vionut	94	6	.3	2	.3	2	1	4	1	.3	2	2	1	2	1	.3	*
Poaref	94	.3	1	.3	3	1	2	2	.3	3	2	.3	.3	1	1	.3	*
Thafen	94	1	1	3	.3	1	.3	4	3	.3	.3	2	1	.3	*	3	.3
Poptre	94	60	80	60	23	60	50	55	70	30	40	35	10	13	15	10	*
Nembre	88	1	.3	1	1	1	13	.3	1	6	2	.3	1	1	1	*	*
Rudocc	88	9	*	12	14	14	24	2	6	10	12	4	.4	.3	9	2	*
Helhoo	88	6	.3	3	3	3	.3	3	2	4	4	2	*	3	4	1	*
Chefre	88	.3	.3	.3	1	1	.3	.3	.3	*	.3	1	.3	*	1	.3	*
Galbif	88	3	*	2	5	1	5	.3	.3	5	4	.3	3	1	1	.3	*
Descal	88	.3	*	.3	.3	2	.3	*	1	.3	.3	1	.3	.3	.3	.3	.3
Osmdep	88	*	.3	5	.3	.3	2	*	2	1	5	4	5	4	6	7	1
Ribmon	81	*	2	.3	*	.3	.3	*	47	.3	.3	1	8	3	26	8	.3

APPENDIX. Continued

Species Code	Constancy (%)	Study stands 105	111	112	103	108	116	109	215	202	204	207	206	201	214	213	210
Collin	81	3	*	.3	1	4	8	7	2	.3	.3	1	.3	*	2	.3	*
Hydcap	81	.3	*	1	.3	1	.3	*	.3	.3	1	.3	.3	1	1	.3	*
Hacflo	81	*	.3	3	*	3	7	.3	4	4	3	6	.3	4	7	.3	*
Samrac	75	*	*	.3	*	33	16	1	7	14	4	13	.3	3	18	.3	*
Bromus	75	1	*	4	2	2	2	6	.3	1	2	.3	*	*	2	.3	*
Osmocc	75	.3	*	2	1	6	3	2	5	1	3	5	*	1	.3	*	*
Valocc	75	8	.3	16	*	9	3	.3	1	7	6	6	1	*	1	*	*
Ranina	75	.3	*	.3	.3	.3	*	*	.3	.3	.3	.3	.3	.3	.3	.3	*
Melspe	69	.3	.3	1	*	.3	1	.3	*	.3	.3	.3	*	.3	.3	*	*
Agrspp	63	1	.3	.3	1	.3	1	2	.3	*	.3	*	*	*	.3	*	*
Agaurt	63	1	*	12	*	.3	1	.3	4	*	1	6	.3	.3	*	*	*
Merari	63	1	1	5	*	4	*	*	*	2	10	14	5	*	4	1	*
Abilas	56	*	*	*	*	*	*	*	5	10	17	15	23	50	15	15	20
Taraxa	56	1	.3	6	.3	*	*	.3	.3	.3	*	*	*	.3	.3	*	*
Achmil	56	2	*	4	.3	*	.3	*	*	1	.3	*	.3	.3	*	.3	*

APPENDIX. Continued

Species Code	Constancy (%)	Study stands 105	111	112	103	108	116	109	215	202	204	207	206	201	214	213	210
Symore	50	7	.3	1	*	*	*	.3	5	*	*	8	7	*	*	*	.3
Senser	50	6	*	*	*	5	.3	2	*	4	*	2	.3	1	*	*	*
Erispe	50	.3	*	1	.3	*	*	3	.3	*	.3	.3	*	*	.3	*	*
Elygla	44	*	7	11	*	1	*	*	*	1	4	1	1	*	*	*	*
Delbar	44	.3	*	*	*	2	.3	.3	.3	*	*	*	*	*	9	2	*
Polfol	44	*	*	.3	*	.3	.3	*	2	.3	*	.3	.3	*	*	*	*
Asteng	44	.3	.3	*	*	1	*	*	.3	*	.3	.3	5	*	*	*	*
Erygra	44	2	*	*	.3	*	.3	.3	*	*	.3	*	.3	.3	*	*	*
Aqucoe	44	*	.3	*	.3	*	*	*	.3	*	.3	.3	1	*	*	*	3
Delnel	38	.3	*	*	.3	*	.3	1	*	*	.3	*	*	.3	*	*	*
Andsep	38	.3	*	*	*	*	*	*	*	1	*	.3	.3	.3	*	.3	*
Lomdis	38	2	*	*	*	*	4	*	8	*	.3	*	6	*	.3	*	*
Herlan	31	*	*	*	*	7	1	*	.3	*	*	24	7	*	*	*	*
Poldou	31	*	.3	*	*	3	*	*	.3	*	*	.3	*	*	.3	*	*
Phahas	31	*	3	*	*	.3	*	*	.3	*	*	*	*	*	.3	1	*

APPENDIX. Continued

Species Code	Constancy (%)	Study stands															
		105	111	112	103	108	116	109	215	202	204	207	206	201	214	213	210
Colpar	31	1	*	*	.3	*	.3	*	*	.3	*	*	.3	*	*	*	*
Carhoo	25	*	*	7	*	*	*	*	*	.3	*	*	.3	*	*	.3	*
Actrub	25	*	*	*	*	14	*	*	*	*	*	2	.3	*	*	2	*
Gerric	25	*	*	*	*	1	*	*	*	*	*	2	1	*	*	6	*
Vigmul	25	3	*	*	.3	*	*	.3	.3	*	*	*	*	*	*	*	*
Potspp	25	.3	*	*	*	*	.3	*	*	*	*	*	.3	*	*	1	*
Viocan	25	*	*	*	*	*	*	*	2	*	*	.3	*	*	1	3	*
Epiang	25	*	*	*	*	*	*	*	.3	*	*	*	*	*	.3	.3	1
Piceng	19	*	*	*	*	*	*	*	*	*	*	*	*	*	.3	25	65
Madglo	19	.3	*	*	1	*	*	1	*	*	*	*	*	*	*	*	*
Clalan	19	*	*	*	*	*	*	*	*	.3	.3	*	*	.3	*	*	*
Penwhi	19	*	1	*	*	*	*	*	1	*	*	*	*	*	*	.3	*
Brocil	13	*	1	*	*	*	*	*	*	*	*	*	*	*	*	*	.3
Cargey	13	*	3	*	*	*	*	*	*	*	*	*	*	*	*	*	.3
Casrhe	13	*	*	*	*	*	*	*	.3	*	*	*	*	*	*	.3	*

APPENDIX. Continued

Species Code	Constancy (%)	Study stands															
		105	111	112	103	108	116	109	215	202	204	207	206	201	214	213	210
Mitsta	13	*	*	*	*	*	*	*	*	*	*	*	*	*	*	.3	1
Vaccae	6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	8
Pacmyr	6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	2
Arncor	6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	7
Pyrsec	6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	7
Fragar	6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	1
Haplop	6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	2
Phlalp	6	.3	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Poapra	6	*	*	*	*	*	*	*	*	.3	*	*	*	*	*	*	*
Lpinus	6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	.3	*
Tradub	6	*	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*
Casspp	6	*	1	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Galbor	6	*	2	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Smiste	6	*	.3	*	*	*	*	*	*	*	*	*	*	*	*	*	*

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