Birds

AVIAN POPULATIONS AND HABITAT USE IN INTERIOR ALASKA TAIGA.

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ABSTRACT

Avian community structure, habitat occupancy levels, and species habitat use patterns were examined in the woody habitats of interior Alaska taiga. Forest habitats, especially coniferous forests, were depauperate during the breeding season compared to temperate forests or more southern portions of the boreal forest of North America, but tall shrub thickets were comparatively rich; relative densities were reversed for permanent resident species. Avian differences among habitats were correlated with differences in primary productivity and structural complexity of the vegetation. The amount of annual variation in numbers of individuals of a species during the breeding season was inversely correlated with its overall abundance.

Most bird species exhibited distinct habitat preferences during the breeding season, and a simple bivariate ordination, using canopy thickness and distance between trees (or density of stems in the medium and tall shrub layers), served to separate the habitats of species groups and of species within groups. Some birds selected habitats different from those used elsewhere in North America, e.g., Hammond's Flycatcher, Hermit Thrush, and Yellow-rumped Warbler were primarily birds of the deciduous forests in interior Alaska.

Key Words: Alaska, taiga, avian community, habitat selection, avian populations.

INTRODUCTION

Avian community structure, habitat occupancy levels, and species habitat use patterns were studied in taiga habitats of the upper Tanana River Valley, east-central Alaska, during the summers of 1975 and 1977. Few quantitative data have been available on the use by birds of taiga habitats in northwestern North America. Populations and energetics in two upland taiga communities of mixed vegetation types near Fairbanks were examined by West and DeWolfe (1974); population density and diversity and avian habitat selection in five lowland taiga mosaic vegetation types near Fairbanks were studied by Spindler (1976); and species composition, abundance, and some structural components of bird populations in eight vegetation communities in the Kluane National Park, southwest Yukon Territory, were studied by Theberge (1976). In a more comprehensive work, Erskine (1977) summarized available data and discussed the density, diversity, and distribution of avian populations throughout much of the boreal forest region of Canada, but his study sites came north only to the Fort Nelson lowlands in northeastern British Columbia (58°49'N, 122°39'W), over 1000 km southeast of our study area.

STUDY AREA

The upper Tanana River Valley region includes the lowlands of the wide valley floors of the Chisana, Nabesna, and upper Tanana rivers (elev. 485-525 m) and the adjacent uplands of the Tanana-Yukon Highlands (elev. > 525 m). The region is within the northern zone of the taiga (Viereck 1975) and supports a variety of widely distributed vegetation types. The uplands contain all stages of forest succession, from sapling stands to mature forests of Quaking Aspen (Populus tremuloides)*, Balsam Poplar (P. balsamifera), Paper Birch (Betula papyrifera), White Spruce (Picea glauca), and Black Spruce (Picea mariana). Extensive pure stands of Quaking Aspen and Black Spruce are common; the other trees also occur in pure stands, but forests of mixed composition are more frequent. Poorly drained upland valley bottoms often contain extensive bogs and shrub thickets (mostly willow and alder) in addition to forests, woodlands, and dwarf forests. The lowlands are a mosaic of wetlands (rivers, lakes, ponds, and marshes), meadows, and bogs in addition to shrub thickets, woodlands, and forests in various stages of succession. The complex patterns of vegetation types in the taiga arise from such inter-

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*Plant nomenclature follows Hultén (1968), with the exception of the genus Salix, which follows Viereck and Little (1972). English names of birds follow the American Ornithologists' Union's Check-list of North American Birds and supplements (1957, 1973, 1976).

related factors as fire, permafrost, alluviation, soil type, slope, aspect, and water relations (Viereck 1970, 1973, 1975).

Approximately 42% of the total area of the upper Tanana River Valley region is covered by Coniferous and Mixed Deciduous-Coniferous forests, 35% by shrublands, 15% by Scattered Woodlands and Dwarf Forests, and 6% by Deciduous Forests (percentages, according to avian habitats [see below], derived from data in Hutchinson 1967 and Hegg and Dippold 1973).

The main research plots for this study were between Tetlin Junction (63°19'N, 142°36'W) and the airport at Northway (62°58'N, 141°56'W). Supplemental data have been added from several lowland taiga plots near Fairbanks, 360 km down the Tanana River Valley.

METHODS

Census plots were selected in each of the six major woody habitats present in the upper Tanana River Valley. Habitats were classified according to Kessel (1979), except that the three lower height shrub layers ($\leq$ 2.4 m), which rarely occurred in homogeneous stands large enough to census quantitatively, were combined into a single habitat of Low and Medium Shrub Thickets.

Within each of the major habitats, we censused birds and sampled vegetation and physical features in several plots in prevalent vegetation types typical and representative of that major habitat. Large homogeneous stands able to encompass a 10-hectare census plot were difficult to locate, but at least one such plot was established in each major habitat. In addition, a number of smaller "miniplots" (1.6-5.8 ha) were established to increase sample size and the variety of vegetation types that could be sampled, even though we recognized that small census plots are generally undesirable because of edge effect and high variability (Oelke 1966, Erskine 1977).

Four 10-ha plots and 15 miniplots were studied in the Tetlin Junction-Northway area in 1977, and data from three 10-ha plots and two miniplots near Fairbanks, obtained in 1975 by Spindler (1976), have been incorporated where applicable.

Bird Censusing

We used a modification of the territory mapping census method (International Bird Census Committee 1970). Each 10-ha census plot was subdivided by a 7x7 grid, resulting in forty-nine 0.2-ha subplots; miniplots consisted of seven to ten 0.2-ha subplots. In all, 331 subplots were censused in 1977, and some data have been used from 196 subplots censused in 1975.

During a census, the observer stopped at the center of each subplot for 2-7 minutes, depending upon avian activity, and recorded all birds seen or heard. For birds seen, activity, height of bird, and plant species used were also recorded. Each census of a 10-ha plot took approximately 4 hours, usually between 0300-0800 (Alaska Standard Time), which is generally within the time of greatest singing activity. Eight censuses were completed on each 10-ha plot between 29 May and 9 July

1977. Censuses were conducted in pairs of two consecutive days at each plot in an attempt to minimize the effects of changing territorial boundaries. Census methods on the miniplots were identical to the 10-ha plots, except that censusing started 13 June and was completed 13 July 1977. Six to nine censuses were completed on each miniplot.

In addition to determining the number of breeding territories of each species, we also recorded non-territorial and non-breeding birds and calculated an index of abundance based on the mean number of birds observed per census. This index was used to compare abundance of permanent resident non-territorial species or those that bred asynchronously from the majority of summer resident species.

Densities on the miniplots were extrapolated to a 10-ha basis and, using a linear regression equation, were adjusted for edge effect and other confounding effects of small plot size. Miniplots were generally near 10-ha plots in similar vegetation types, so we were able to develop the regression equation for each vegetation type to identify the relationship between density of each species/miniplot and density/10-ha plot. In determining mean population characteristics of a habitat, miniplots and 10-ha plots were treated equally.

Habitat Description

The bird census subplots were used as sample units in vegetation analyses. Two systematically located points in each subplot were sampled, using the point-centered quarter method of Cottam and Curtis (1956), but including more detailed sampling of ground cover, understory, and shrub vegetation. Fifty-one variables were measured at each sample point.

In using the point-centered quarter method, all measurements were based on selection of the nearest stem $\geq$25.4 mm in diameter. This stem sample was used to calculate species relative importance values and for values of height, diameter, basal area, and height distribution of foliage volume and stem density. Percent ground cover for each of six categories--grass, forb, moss and lichen, dwarf shrub, forest litter, and water--was estimated visually inside a 1 m radius circle around the sample point, and ground cover species were recorded and analyzed for frequency of occurrence. Evidence of fire and edge were quantified as a 0-1 index; aspect was measured with a compass. Slope and stem height were measured with an Abney level. Canopy thickness was the distance between the top of the stem and its lowest live branch. Brush density was measured as the number of stems intercepted by a 1 m radius circle 1 m above ground. Percent canopy cover was estimated as the amount of sky obscured by foliage as viewed from 1 m above ground through a 100 mm diameter circle. Stand ages were determined by increment borer samples from at least seven of the largest stems on each plot.

On the Northway plots measured stems of varying heights were classified into three height intervals, corresponding to layers characteristic of interior Alaska habitats--1.2-2.4 m (medium shrub), 2.5-4.9 m (tall shrub), and $\geq$ 5.0 m (tree). Foliage volume was quantified with a 5.0 m-tall stick marked according to the three height classes; an imaginary cylinder 1 m in radius was circumscribed around the stick, and the percent of total volume occupied by foliage within each of the three height classes comprising the cylinder was visually estimated.

Relative importance values were calculated as the sum of relative frequency, relative density, and relative dominance of the species in the stand (Curtis and McIntosh 1951) divided by three.

Analytical Techniques

The avian communities in the major habitats were compared relative to species composition, species richness, breeding density, breeding biomass, existence energy, dominance index, and species abundance distribution (density-dominance structure). For comparability with other studies, we calculated a species diversity index, H' (Shannon and Weaver 1949, Pielou 1975). Since breeding species diversity was highly correlated with the number of species ($R^2 = 0.61$, $n = 23$, $p < 0.001$), a phenomenon also reported by Tramer (1969) and Austin and Tomoff (1978), we chose to base our diversity analyses solely on the number of species (species richness), a less complex measure. Dominance index was defined as the percent of total density comprised by the two most abundant species (McNaughton 1967, Wiens and Dyer 1975).

Breeding biomass for each species was calculated as the product of breeding density and mean weight. Species weights used were the mean weight for all adult specimens in the University of Alaska Museum that had been collected in Alaska during the breeding season. When the museum sample was too small, or variability too high, we consulted published literature (Carbyn 1971, West and DeWolfe 1974) for values determined from northern populations. On plots with large-bodied breeding birds (e.g., cranes, waterfowl, grouse, or raptors), we apportioned the biomass according to estimated territory or "home range" sizes obtained from local field observations and the literature, to prevent artificially high biomass extrapolations arising from small plot data. In several instances, the territory of a pair of heavy-bodied birds centered on a plot (Spruce Grouse in plot CF3 and Great Horned Owl on plot DF5) and even with apportionment skewed the total biomass disproportionately; these birds were eliminated entirely from the biomass calculations. Breeding biomass for each species, expressed as grams of breeding birds per 10 ha, was used to calculate existence energy. Existence energy (sometimes referred to as metabolic density or consuming biomass) is an approximation of daily energy requirements. For each species in each major habitat, we calculated existence energy (M) as $M = D \cdot W^{0.76}$, where "D" was density in breeding birds per 10 ha and where "W" was the average weight, determined as explained above. This method of estimating the daily energy expenditure in kilocalories (kcal) for the maintenance of bird biomass admittedly is rough, but it is adequate for comparisons of general community patterns (Karr 1968). Calculations made by raising bird weight to a fractional exponent produce a better index of energy flow than breeding biomass alone by accounting for the lower metabolic rates of large-bodied birds (Salt 1957, Karr 1968, Kendeigh 1970).

Similarities of species composition among the 23 plots were compared with a cluster analysis (Biomedical Computer Program BMDP1M [Dixon and Brown 1979]), using a matrix of similarity coefficients which reflected the proportion of species shared by pairs of plots (Sørenson 1948).

Bird species that occurred on ten or more subplots were examined for patterns of habitat use. In statistical analyses of avian habitat use, we emphasized the description of the habitats used by a species, rather than the ranking of the predictive value of particular variables. Univariate one-way analysis of variance (Steel and Torrie 1960) was used to determine which habitat variables differed significantly between groups of subplots where a species occurred (species-present habitats) and where it did not occur (species-absent habitats) (Anderson and Shugart 1974). For the purposes of habitat description, univariate analysis of variance (ANOVA) provided more descriptive information than did multivariate stepwise regression (REGRN) and stepwise discriminant analysis (DFA). ANOVA independently evaluates all variables, usually identifying several significant habitat characteristics which may or may not be intercorrelated. The multivariate techniques select sequentially the single best predictive variable, but discard other descriptive variables that are highly correlated with any already selected in the model. The univariate F-ratio from ANOVA is by definition proportioned to the correlation of a variable and its discriminant function in a multivariate ANOVA if two groups are involved (Anderson and Shugart 1974). Hence, the size of the univariate F-ratio may be used as a general indicator of the relative importance of a variable in distinguishing between species-present and species-absent groups.

Of the original 51 habitat variables measured, 15 were not used in statistical analyses because they (1) were redundant, (2) could be consolidated into fewer categories, (3) were not continuous or ordinal, or (4) showed excessively skewed or kurtotic distributions. The remaining 36 variables were included in a one-way ANOVA to compare the species-present and species-absent habitats for each of 26 bird species. A total of 936 separate analyses of variance were performed using Biomedical Computer Program BMDP7D (Dixon and Brown 1979).

Stepwise multiple regression (Draper and Smith 1966) was used to order habitat variables (independent variables) according to effectiveness in predicting bird density on subplots and predicting biomass and existence energy on entire census plots (Statistical Analysis System [Service 1972] and Biomedical Computer Program BMDP2R [Dixon and Brown 1979]). Stepwise discriminant function analysis (Morrison 1976) in the form of a multivariate analysis of variance was used to identify the two or three significant variables that could best separate the species-absent and species-present groups and groups of bird species common to a habitat type (Biomedical Computer Program BMDP7M [Dixon and Brown 1979]).

Principal components analysis (Morrison 1976) was used to determine the relative position of each species along environmental gradients. This analysis is capable of reducing multivariate data to a few dimensions which "... are the linear combinations of the original variables that successively account for the major independent patterns of variation in the sample" (Bryant and Atchley 1975:3). Each of the dimensions, or principal components, accounts for a unique and successively smaller portion of the total variance within the data set. A data set of 21 habitat variables, which were continuous and primarily structural habitat characteristics of each subplot, was weighted according to the subplot's apparent favorability as a habitat for each species (i.e., the data set for each subplot was duplicated for each time an individual of the species was seen on that subplot). This weighting resulted in the creation of a 4786-case data array for the 26 bird species. This array was subjected to a principal components analysis based on a correlation matrix using the SPSS Factor program (without rotation) (Nie et al. 1975). The weighted array for each bird species was then scored against (i.e., projected onto) the resulting first three principal components to determine the relative position of each species in the habitat space defined by the three components.

HABITAT DESCRIPTIONS

Several bird census plots were established in vegetation types representative of each of the six woody habitats present in the upper Tanana River Valley. Values of the most diagnostic variables for these plots are given in Table I. A description of each habitat follows:

Low and Medium Shrub Thickets (LMS)

Open or closed shrub stands of willow, alder, or dwarf birch (<u>Betula</u> sp.) ≤ 2.4 m in height comprise the Low and Medium Shrub Thickets habitat (Fig. 1 and Table I). Usually extensive dwarf shrub, grass, sedge, or wet-sedge ground cover are associated with these habitats. Most such

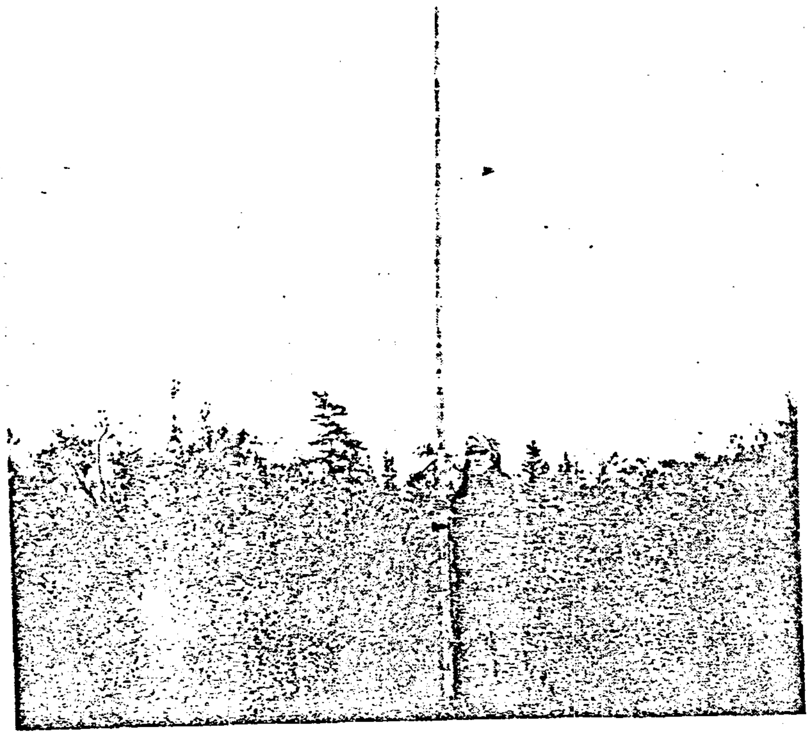

Figure 1. Low and Medium Shrub Thickets. Plot LMS2, Upland Low and Medium Willow, Milepost 1280, Alaska Highway, August 1977.

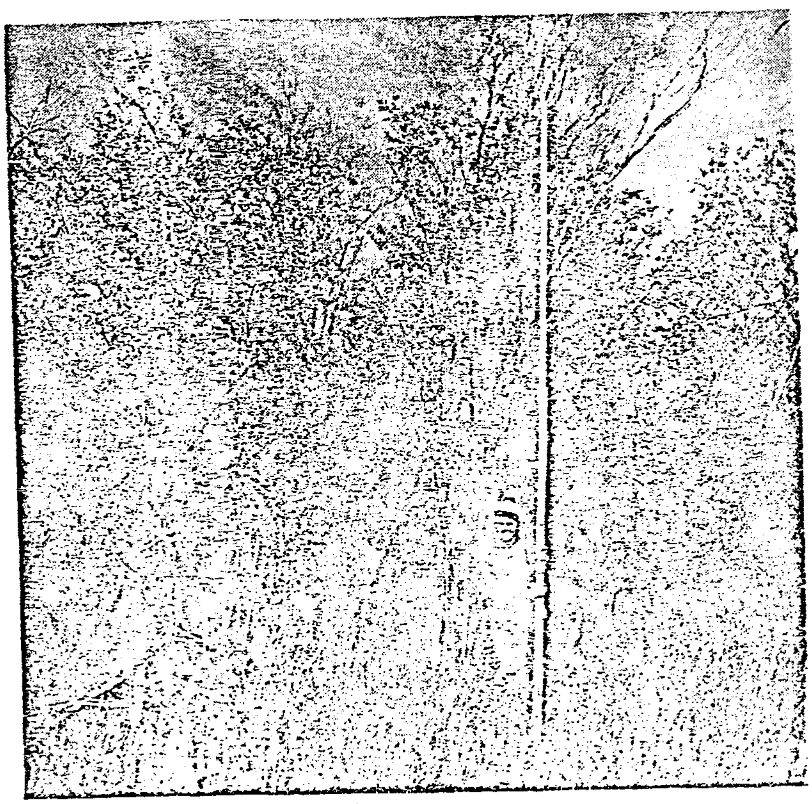

Figure 2. Tall Shrub Thicket. Plot TS3, Upland Tall Willow, Milepost 1281, Alaska Highway, August 1977.

shrub habitats are relatively permanent habitats in which the vegetation is stunted by rigorous growing conditions (Drury 1956, Viereck 1975, Calmes 1976).

Three of these shrub thickets were sampled, two in lowland river flats and one (LMS2) in an upland valley bottom. All plots were flat and poorly drained. Shrub growth consisted of 1-2 m-tall willows (Salix planifolia, S. arbusculoides, S. glauca, S. novae-angliae, and S. candida). Ground cover in two of the plots (LMS2 and LMS3) was primarily Eriophorum vaginatum tussocks, with dwarf shrubs growing between and on top of the tussocks; dwarf shrub species included Betula nana, Vaccinium vitis-idaea, V. uliginosum, Ledum palustre, Chamaedaphne calyculata, and Salix myrtillifolia. Ground cover on plot LMS1 was wet-sedge meadow (mostly Carex sp.), with some areas of dry site forbs, Equisetum sp., and Calamagrostis canadensis. All three plots had occasional stunted tree or tall shrub species--white spruce, black spruce, paper birch, thinleaf alder (Alnus incana)--up to 6 m tall.

Tall Shrub Thicket (TS)

Open or closed shrub stands 2.5-4.9 m in height comprise the Tall Shrub Thicket habitat (Fig. 2 and Table I). Most tall shrub habitats are composed of willow and alder and occur in valley bottoms; however, moist hillsides and timberline areas also have extensive tall shrub stands.

Sampled Tall Shrub Thickets included two types: lowland riparian thickets (TS1 and TS4), probably maintained by frequent flooding and permafrost, and upland successional stages of the White Spruce fire sere (TS2 and TS3). Dominant components of the lowland stands were thinleaf alder, Salix arbusculoides, S. planifolia, S. bebbiana, and S. novae-angliae. The upland thickets had a predominance of S. alaxensis, S. monticola, and balsam poplar, with interspersed S. bebbiana, S. arbusculoides, and S. planifolia. Major ground cover species common to both types were Calamagrostis canadensis and Ledum palustre. Comparatively, the lowland plots had more Equisetum silvaticum, Rubus arcticus, and Vaccinium uliginosum, whereas the upland plots had more V. vitis-idaea, Epilobium angustifolium, and Arctostaphylos uva-ursi.

Deciduous Forests (DF)

Deciduous Forests are closed stands of trees >5.0 m high composed of quaking aspen, balsam poplar, or paper birch (Fig. 3 and 4, Table I). Most deciduous forests occur as successional stages on upland slopes following fire or in well-drained floodplains. Aspen stands generally occur on steep, south-facing xeric slopes, while paper birch stands occur on more mesic slopes. Both may occur on adequately drained sites in the lowlands, such as on terraces or eskers. Balsam poplar occurs in pure stands on well-drained floodplains and in mixed stands with aspen in the uplands.

Three aspen-dominated and two birch-dominated stands were sampled, all seral stages following fire 60-100 years ago. Two of the aspen plots (DF1 and DF2) were in nearly mature, open, park-like stands, with some poplar intermixed. The third plot (DF3) consisted of a much denser,

Figure 3. Deciduous Forest, Aspen-dominant stand. Plot DF2, Upland Aspen #1, Milepost 1274, Alaska Highway, August 1977.

Figure 4. Deciduous Forest, Birch-dominant stand. Plot DF4, Upland Birch #1, Milepost 1275, Alaska Highway, August 1977. Note the understory of Mountain Alder.

younger, and smaller diameter pure aspen stand, with occasional *Salix bebbiana* and *S. scouleriana*. All aspen plots had a characteristic understory of the fleshy fruit-producing shrubs *Shepherdia canadensis*, *Viburnum edule*, *Vaccinium vitis-idaea*, *Rosa acicularis*, and *Arctostaphylos uva-ursi*. Many of the fruits remained overwinter and were utilized by birds the following summer.

The birch-dominated stands (DF4 and DF5) were both mature and had mountain alder, *Salix bebbiana*, and *S. scouleriana* as understory and occasionally co-dominant species. Ground cover was more luxuriant than in aspen stands, including dense low shrub cover of *Rosa acicularis*, *Viburnum edule*, and *Ribes* sp., and rank growth of *Calamagrostis canadensis*, *Equisetum silvaticum*, and *Mertensia paniculata*. Birch stands lacked the more prolific berry-producing species.

Mixed Deciduous-Coniferous Forest (MF)

Mixed Deciduous-Coniferous Forest habitat is comprised of closed stands of deciduous and coniferous trees ≥5.0 m tall, generally containing mixtures of one or two deciduous tree species and either white spruce or black spruce (Fig. 5 and Table I). Generally, such mixtures represent stages of succession in which spruce is replacing the deciduous tree species (Viereck 1975).

All five mixed plots showed evidence of fires within the last 50-130 years, but were each quite different in stand composition and structure. Four of the plots were in upland habitats (MF1, MF2, MF3, and MF5), and

Figure 5. Mixed Deciduous-Coniferous Forest. Plot MF2, Upland Birch-White Spruce, Milepost 1265, Alaska Highway, August 1977.

one was in a lowland river basin (MF4). Plot MF1 was dominated by quaking aspen and white spruce, with some balsam poplar. Plot MF3 was a diverse mixture of white spruce, quaking aspen, and paper birch, with a thick understory of *Salix bebbiana* and mountain alder. Plot MF2 was dominated by paper birch and white spruce, with the understory of mountain alder characteristic of moist birch sites. Plot MF5 was a dense sapling stand of paper birch with a few large white spruce. The lowland mixed Plot MF4 was dominated by white spruce and black spruce, with scattered paper birch, and supported a dense understory of willow (*S. arbusculoides*, *S. planifolia*, and *S. bebbiana*) on the drier portions. A small creek lined with thinleaf alder flowed across the plot. Ground cover species consistently present in all mixed habitats were *Rosa acicularis*, *Mertensia paniculata*, *Geocaulon lividum*, *Calamagrostis canadensis*, *Linnaea borealis*, and *Equisetum scirpoides*. Other ground cover and understory characteristics varied along a moisture gradient from the more xeric S-facing steep plots (MF1 and MF3), to mesic E- or W-facing gentle hillsides (MF2 and MF5) and wet, valley-bottom sites (MF4). The drier sites had *Shepherdia canadensis* and *Zygadenus elegans*, while more mesic sites included *Viburnum edule*, *Vaccinium vitis-idaea*, *V. uliginosum*, and *Ribes* sp. Abundant moss cover with *Ledum palustre* and *Rubus chamaemorus* was specific to the dampest sites.

Coniferous Forest (CF)

Closed stands of conifers ≥5.0 m high, mostly white spruce and black spruce (Fig. 6 and 7, Table I) but with occasional stands of

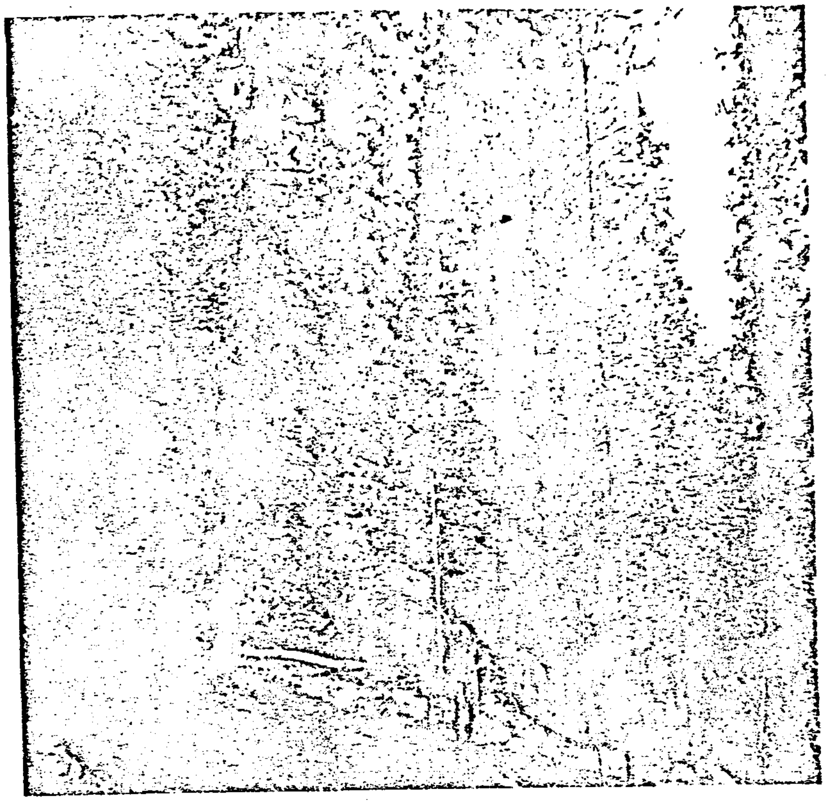

Figure 6. Coniferous Forest, White Spruce-dominant stand. Plot CF1, Upland White Spruce #1, Milepost 1299, Alaska Highway, September 1977.

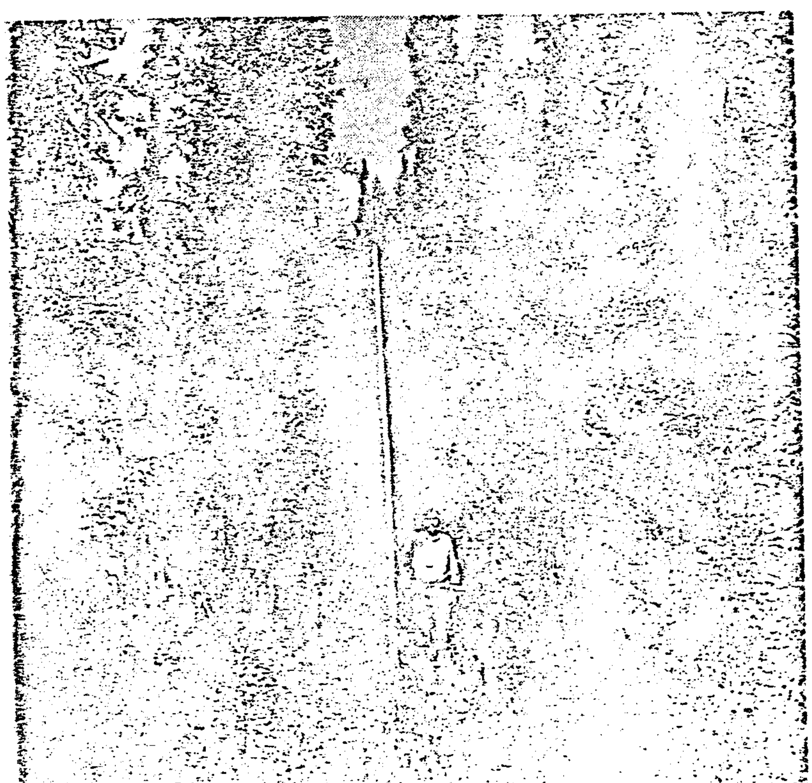

Figure 7. Coniferous Forest, Black Spruce-dominant stand. Plot CF3, Upland Black Spruce, Milepost 1299, Alaska Highway, September 1977.

tamarack (Larix laricina), comprise the Coniferous Forest habitat. Understory shrubs are usually sparse, and moss frequently dominates the ground cover. White spruce occurs in pure stands on well-drained sites, such as steep south-facing slopes and on sand and gravel in river floodplains. Black spruce may form relatively tall (to 12 m), dense stands on moderately-drained sites in the lowlands and on N, NE, NW-facing slopes in the uplands. Black spruce gradually replaces white spruce in river valleys through a bog-forming (paludification) process lasting 200-250 years (Drury 1956, Viereck 1970). Tamarack occurs in the lowlands, most frequently on wet sites. White spruce forests occasionally form majestic stands of 40 m tall, 1 m dbh trees, which, along with the black spruce bog-forests on poorer sites, are considered to be climax stages of forest succession in interior Alaska.

We sampled Coniferous Forests at three upland sites (CF1, CF2, and CF3) and one lowland site (CF4). Plot CF1 was an extensive, mature white spruce stand growing on a steep south-facing slope. Occasional black spruce trees occurred on the lower side, and scattered aspen trees blended in on one upper corner. Plot CF2 was similar, except the white spruce were denser and smaller, with occasional paper birch and mountain alder in the understory. Plot CF3 was dominated by black spruce, with widely scattered white spruce. Plot CF4 was similar to CF3, but with the addition of tamarack in wetter portions. As with the Mixed Deciduous-Coniferous Forests, ground cover and understory varied with moisture: Linnaea borealis, Geocaulon lividum, Calamagrostis canadensis, and Rosa acicularis were characteristic of the drier, white spruce habitats, while Rubus chamaemorus, Vaccinium uliginosum, Ledum palustre, Petasites hyperboreus, and Sphagnum moss were prominent on the moister black spruce sites.

Scattered Woodland and Dwarf Forest (WD)

Open stands of stunted trees spaced so that most tree crowns do not touch each other are the main characteristics of the Scattered Woodland and Dwarf Forest habitat. Such habitats are termed "Dwarf Forest" if the height of trees is <5.0 m and "Woodland" if ≥5.0 m (Fig. 8 and 9, Table I). This habitat is a "hybrid" habitat with both shrub thicket and forest habitat characteristics, and as such, it is more variable and generally more spatially heterogeneous than the other forest habitats. A sizable proportion of interior Alaska woody habitats fall into this category, mainly because of extensive forest-tundra ecotone areas and stunted tree bogs.

Three stands were sampled, a White Spruce-Birch Woodland and two Black Spruce Bogs. The woodland (WD1) was dominated by widely-spaced stunted white spruce and had occasional widely-spaced paper birches. Both dwarf forests were stunted Black Spruce Bogs, one in the uplands (WD2) and one, which included occasional tamarack trees, in an alluvial lowland (WD3). Permafrost was evidently the primary factor involved in the stuntedness of these stands. Ground cover was composed of either extensive Sphagnum moss and/or Eriophorum vaginatum tussocks. Other species consistently present were Vaccinium vitis-idaea, V. uliginosum, Ledum palustre, Eriophorum vaginatum, Chamaedaphne calyculata, and Rubus chamaemorus.

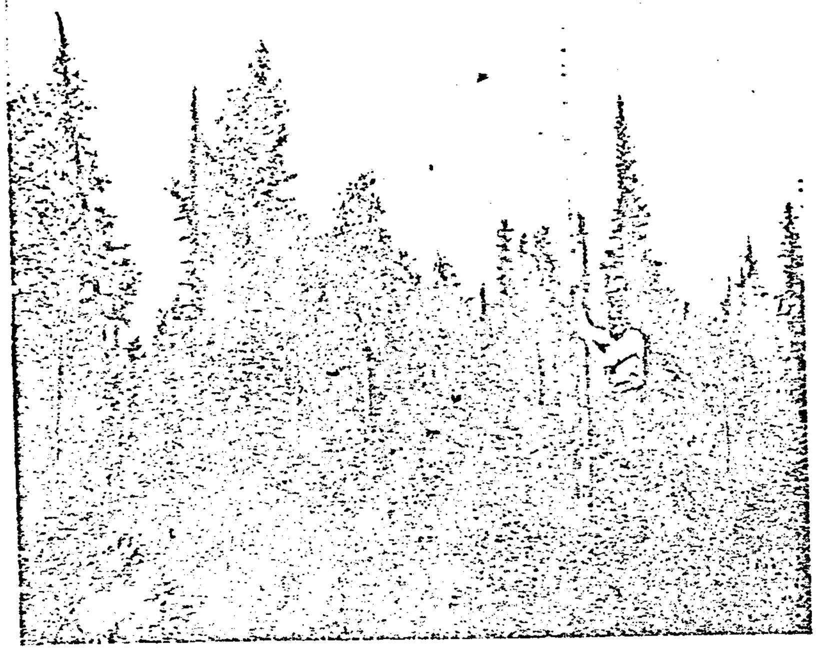

Figure 8. Scattered Woodland and Dwarf Forest. Plot WD1, Lowland White Spruce-Birch Woodland, Northway Airport, August 1977.

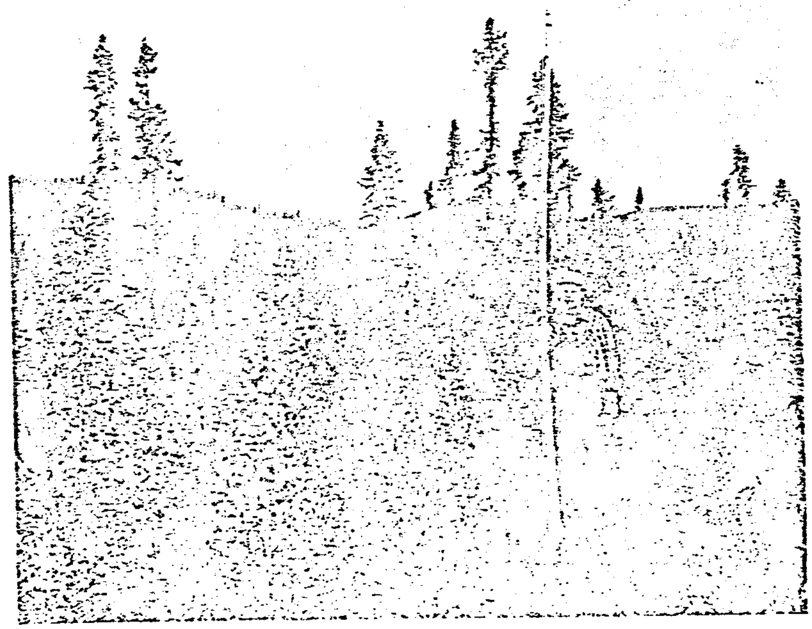

Figure 9. Scattered Woodland and Dwarf Forest. Plot WD2, Upland Black Spruce Bog, Milepost 1285, Alaska Highway, August 1977.

COMMUNITY STRUCTURE AND HABITAT OCCUPANCY LEVELS

Species composition and habitat occupancy* levels differed markedly among the major habitats, but were generally similar among plots within the same habitat (see Tables II and III and Fig. 10). The greatest within habitat differences were between upland and lowland plots. Lowland plots generally had higher densities and more species than upland plots in the same habitat and often had relatively more large-bodied birds, e.g., waterfowl, cranes, and some shorebird species.

A cluster analysis based on similarity indices of species composition among all plots in all of the major habitats is illustrated in Figure 10. Generally, the major compositional division came between shrub thicket and forest habitats, and this division was closely paralleled by a division between upland and lowland habitats. The mixture of plots of different major habitats at the center of the dendrograph, at the base of the two main branches, illustrates the complex interrelationship of these two sets of forces (forest vs. shrub, upland vs. lowland) on avian distribution. Two additional factors were involved in this mixture on the dendrograph. First, as indicated elsewhere, Scattered Woodland and Dwarf Forest (WD) is essentially a "hybrid" habitat between shrub thickets and forests. Second, Lowland Black Spruce (CF4) and Lowland Black Spruce Bog (WD3) were originally a single plot, which we

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*Habitat occupancy is a general term referring to the level of population being supported by a habitat, including number of individuals, density, biomass, and/or existence energy.

SAMPLE FORMAT ONLY

TABLE II

Summary of values of habitat variables from each Deciduous Forest bird census plot, Tanana River Valley, Alaska, August 1975 and 1977

Variable	Upland Aspen-Poplar (DF1)	Upland Aspen #1 (DF2)	Upland Aspen #2 (DF3)	Upland Birch #1 (DF4)	Upland Birch #2 (DF5)
Water, standing (% of ground cover)	0.0	0.0	0.0	0.0	0.0
Stem Diameter (mm dbh)*	131	121	91	123	112
Distance between Stems ≥25.4 mm dbh (m)*	2.9	2.8	1.7	2.9	2.4
Distance between Trees ≥5.0 m height (m)	2.9	2.9	1.7	3.2	2.6
Stem Height (m)	12.0	11.7	10.4	10.4	10.1
Canopy Thickness (m)	6.4	5.4	4.6	7.7	6.3
Total Canopy Coverage (%)	74.3	71.2	75.7	78.6	81.4
Distribution of Foliage Volume (% in each class)					
≥5.0 m	65.2	65.2	66.2	56.2	60.6
2.5-4.9 m	9.1	9.7	9.1	21.2	17.0
1.2-2.4 m	7.6	8.6	7.8	8.6	8.5
0-1.1 m	18.2	16.5	16.9	14.0	13.8
Brush Density, @ 1.0 m (stems$\times10^3$/ha)	6.00	5.69	7.41	7.51	6.00
Height Distribution of Density of Stems ≥25.4 mm dbh (% in each class)					
≥5.0 m (tree layer)	83.9	94.1	87.5	81.1	89.3
2.5-4.9 m (tall shrub layer)	16.1	5.4	12.5	17.6	8.9
1.2-2.4 m (medium shrub layer)	0.0	0.5	0.0	1.3	1.8
Basal Area of Stems ≥ 25.4 mm (m^2/ha)*	20.638	16.868	27.986	18.379	18.752
Tree and Shrub Species Relative Importance (%)*					
White Spruce	0.0	14.3	7.0	2.5	3.9
Black Spruce	0.0	0.0	0.0	0.0	0.0
Paper Birch	0.0	1.1	0.0	53.8	55.9
Quaking Aspen	58.5	72.7	76.6	1.1	0.0
Willow	16.3	9.1	6.3	16.9	24.9
Balsam Poplar	25.2	1.9	10.1	0.7	0.0
Thinleaf Alder	0.0	0.0	0.0	0.0	0.0
Mountain Alder	0.0	0.9	0.0	24.9	15.3
Stand Age (years)					
Mean Age	100	96	59	84	58
Maximum Age	105	107	72	125	76
Index of Stem Heterogeneity**	13.2	22.0	44.1	32.1	32.4
Index of Tree Heterogeneity**	13.2	20.8	44.1	28.4	20.8

*See Cottam and Curtis (1956)

**See Roth (1976)

Community characteristics of avian habitats in the Tanana River Valley, Alaska, breeding seasons 1975 and 1977

	PLOT SIZE (ha)	DENSITY (territories/ 10 ha)	BIOMASS (g/10 ha)	DAILY EXISTENCE ENERGY (kcal/10 ha)	DOMINANCE INDEX (%)	DIVERSITY (# of Breeding species)	(H')	(J')
LOW AND MEDIUM SHRUB THICKETS (LMS)								
1. Lowland Low & Medium Willow	4.25	44.1	4050	1518	39.9	15	2.071	0.765
2. Upland Low & Medium Willow	1.61	27.7	1452	635	71.0	8	1.587	0.763
3. Tussock-Low & Medium Shrub Bog	10.00	23.6	1198	516	57.2	7	1.610	0.828
MEAN ± SD		31.8±11.4	2233±1578	890±547	56.0±15.6	10.0±4.4	1.756	0.785
TALL SHRUB THICKET (TS)								
1. Lowland Tall Alder-Willow	3.35	64.3	3544	1464	41.8	18	2.364	0.818
2. Lowland Tall Willow-Poplar	1.61	67.7	2176	1141	40.6	11	2.036	0.849
3. Upland Tall Willow	1.61	41.8	1896	847	45.9	8	1.781	0.856
4. Lowland Tall Alder-Willow	10.00	58.1	5808	1968	30.1	18	2.584	0.894
MEAN ± SD		58.0±11.5	3356±1786	1355±480	39.6±6.7	13.8±5.1	2.191	0.854
DECIDUOUS FOREST (DF)								
1. Upland Aspen-Poplar	1.61	28.7	1498	642	35.5	10	2.092	0.908
2. Upland Aspen #1	10.00	27.7	2058	792	45.1	13	1.782	0.695
3. Upland Aspen #2	1.61	26.9	1690	700	42.4	8	1.761	0.847
MEAN aspen-dominant ± SD		27.8±0.9	1749±285	711±76	41.0±5.0	10.3±2.5	1.878	0.817
4. Upland Birch #1	10.00	26.9	1386	592	40.9	15	2.104	0.777
5. Upland Birch #2	1.61	25.7	1212	546	43.2	7	1.736	0.892
MEAN birch-dominant ± SD		26.3±0.8	1299±123	569±33	42.1±1.6	11.0±5.7	1.920	0.835
MEAN all deciduous combined ± SD		27.2±1.1	1569±324	654±96	41.4±3.6	10.6±3.4	1.895	0.824

	PLOT SIZE (ha)	DENSITY (territories/ 10 ha)	BIOMASS (g/10 ha)	EXISTENCE ENERGY (kcal/10 ha)	DOMINANCE INDEX (%)	(# of breeding species)	(H')	(J')
MIXED DECIDUOUS-CONIFEROUS FOREST (MF)								
1. Upland Aspen-White Spruce	1.84	35.9	1786	794	54.6	11	1.968	0.821
2. Upland Birch-White Spruce	10.00	36.4	1958	832	48.1	14	1.990	0.754
3. Upland White Spruce-Aspen-Birch	2.20	31.6	1630	703	40.5	8	1.954	0.939
4. Lowland White Spruce-Black Spruce-Birch	10.00	28.6	1602	689	42.0	20	2.323	0.775
5. Upland White Spruce-Sapling Birch	1.61	(0)	(0)	(0)	(0)	(0)	(0)	(0)
MEAN (excluding MF5) ± SD		33.1±3.7	1744±164	755±70	46.3±6.4	13.3±5.1	2.059	0.822
CONIFEROUS FOREST (CF)								
1. Upland White Spruce #1	10.00	26.9	1450	566	48.3	16	1.808	0.652
2. Upland White Spruce #2	1.61	21.3	1080	432	70.9	7	1.363	0.701
MEAN white spruce-dominant ± SD		24.1±4.0	1265±262	499±95	59.6±16.0	11.5±6.4	1.586	0.667
3. Upland Black Spruce	1.61	15.5	682	312	69.7	8	1.489	0.716
4. Lowland Black Spruce	5.75	22.1	1328	563	51.1	11	1.882	0.785
MEAN black spruce-dominant ± SD		18.8±4.7	1005±457	438±177	60.4±13.2	9.5±2.1	1.686	0.751
MEAN all coniferous combined ± SD		21.5±4.7	1135±339	468±121	60.0±12.0	10.5±4.0	1.636	0.714
SCATTERED WOODLAND AND DWARF FOREST (WD)								
1. Lowland White Spruce-Birch Woodland	1.61	37.3	2218	937	31.6	12	2.262	0.916
2. Upland Black Spruce Bog (Dwarf Forest)	1.61	22.2	1126	496	52.3	8	1.773	0.853
3. Lowland Black Spruce Bog (Dwarf Forest)	4.25	20.9	1404	581	67.5	10	1.584	0.688
MEAN Dwarf Forest (excluding WD1) ± SD		21.6±0.9	1265±197	539±60	59.9±10.7	9.0±1.4	1.679	0.771
MEAN all Scattered Woodland and Dwarf Forest combined ± SD		26.8±9.1	1583±568	671±234	50.5±18.0	10±2.4	1.873	0.819

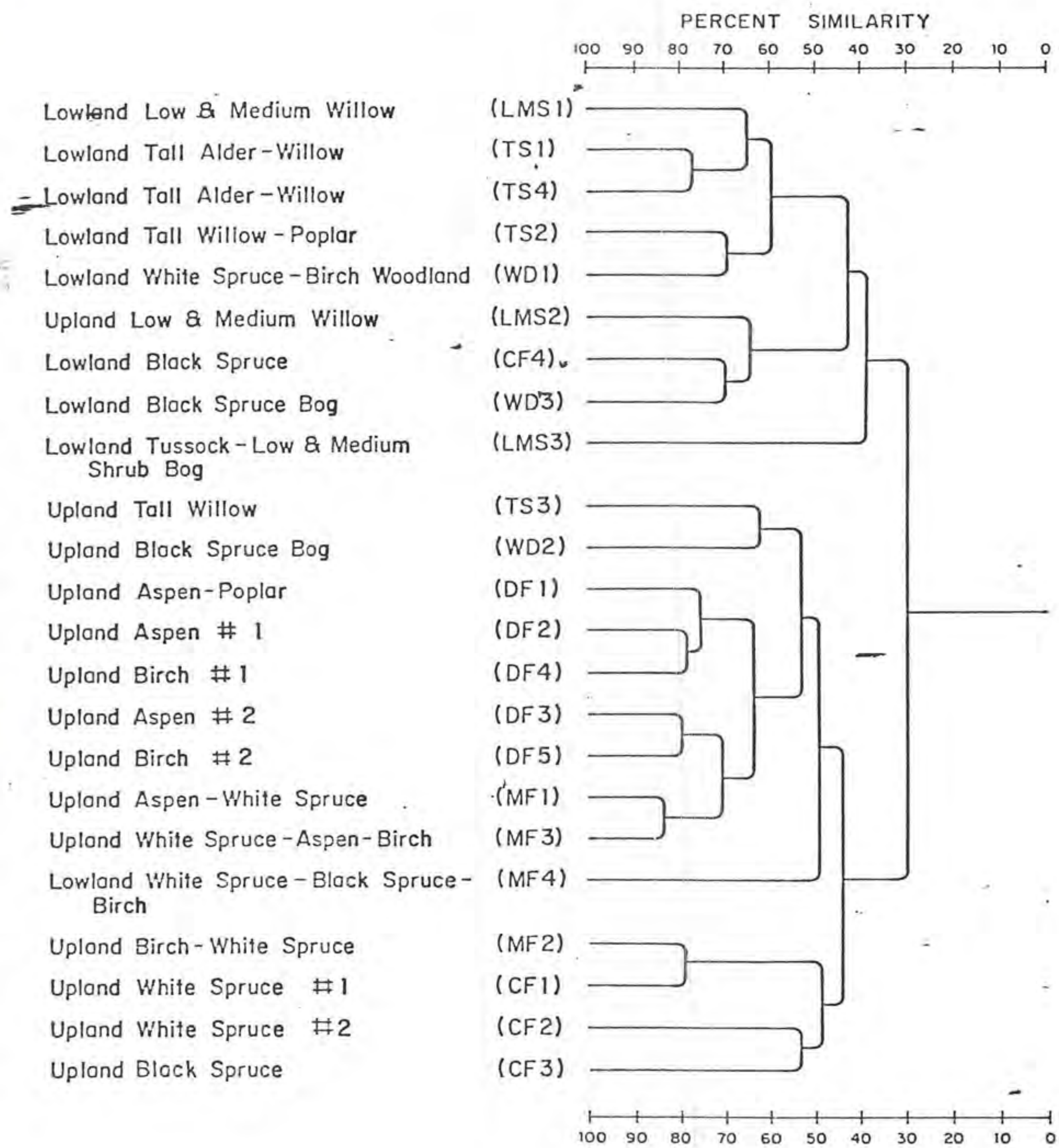

Figure 10. Cluster analysis of bird census plots in the upper Tanana River Valley, based on similarity indices of species composition.

divided for analytical purposes, and the cluster analysis reflects the high species overlap between the two divisions of the plot.

For the most part, habitats supporting high breeding densities also had high species richness and high estimated breeding biomass and daily existence energy (Table III). Sixty-eight percent of the variation in species richness was attributable to variation in breeding density. There was a logarithmic relationship between these two factors (Fig. 11)--i.e., as breeding densities increased, the rate of increase in species richness decreased--a pattern also observed with species diversity by MacArthur (1964) and Karr (1968). Seventy-eight percent of the variability in daily existence energy was attributable to variation in breeding density ($\ln y = \ln 296.68 + 0.027x$, $R^2 = 0.778$, $n = 23$, $p < 0.01$). Stepwise multiple regression and correlation analyses showed that high avian biomass and existence energy were associated with tall shrubs, water, openness, thinleaf alder, and balsam poplar.

Lowland shrub thickets on the study area had the greatest values for existence energy, while coniferous vegetation types showed the lowest (Table III). Ranking of habitats and vegetation types according to total existence energy was lowland Tall Shrub Thicket > lowland Low and Medium Shrub Thickets > lowland White Spruce-Birch Woodland > Mixed Deciduous-Coniferous Forest > aspen stands > birch stands > Black Spruce Bog > white spruce stands > black spruce stands. This habitat ranking was highly correlated with the primary productivity levels of corresponding interior Alaska forest and shrub stands as determined by

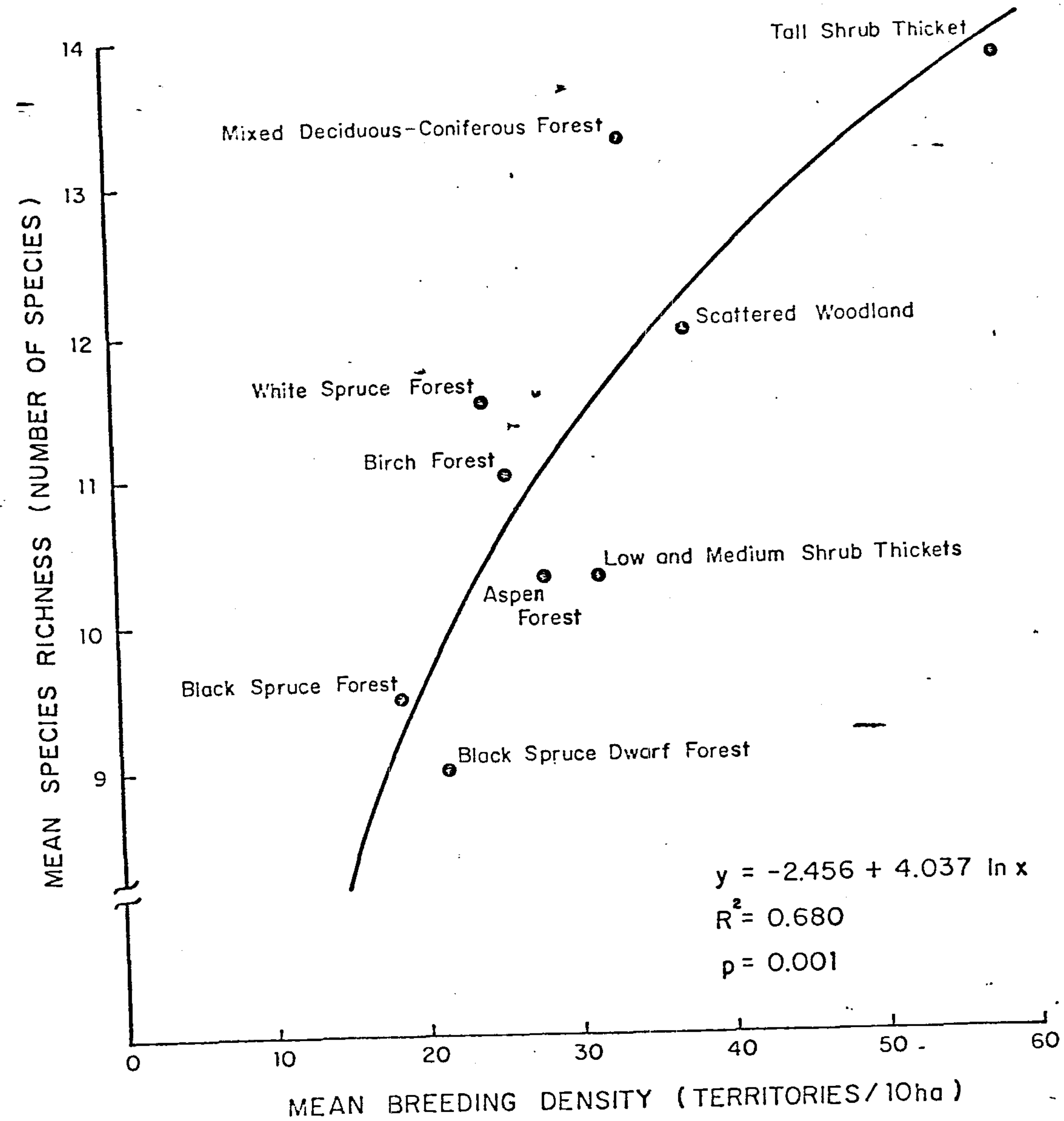

Figure 11. Logarithmic relationship between breeding density and species richness for the major woody avian habitats and subtypes of the upper Tanana River Valley, Alaska.

Van Cleve and associates (Table IV) (Spearman's rank correlation r_s=0.90, n = 5, p < 0.02). Lowland thinleaf alder showed by far the highest annual primary productivity of any woody plant species, and we found the highest species richness and estimated existence energy in tall shrub stands with thinleaf alder (TS1 and TS4). Conversely, coniferous forests, especially black spruce stands, showed the lowest primary productivity levels and had the lowest estimates of avian existence energy and species richness. A comparison of habitats through analysis of density-dominance structures (Fig. 12), existence energy-dominance structures (Fig. 13), partitioning of existence energy among foraging guilds (Table V and Fig. 14), and vegetation structure elucidates many of the community differences observed among the habitats.

The patterns of resource allocation indicate whether avian richness resulted from the addition of foraging guilds or from the expansion of guilds (Fig. 14). A straight line suggests either a community of a few niche-isolated species or a more diverse community exhibiting niche pre-emption--with the steepest-sloped lines indicating higher degrees of dominance (MacArthur 1957, 1960; Whittaker 1965, 1975). A sigmoid-like curve, depending on its form, suggests various levels of partial competition, with the more horizontal curves indicating a number of species of intermediate abundance having no great competitive advantage over the others, either because of niche separation (Whittaker 1965) or ample resources (Wiens 1977). A few relatively dominant species will cause a steeper slope at the top of the curve, as will a small number of rare species at the bottom of the curve. The higher the species diversity of the community,

TABLE IV

Primary productivity of trees and shrubs, based on annual biomass production of foliage, Fairbanks, Alaska. Data from Van Cleve et al. (1971) and unpublished records of K. Van Cleve and C. T. Dyrness, Forest Soils Laboratory, University of Alaska.

	Age of sampled stands (years)	Mean height of sampled plants (m)	Total foliage biomass (gm/m^2)	Av. foliage biomass per meter of plant height*
Thinleaf alder (lowland)	5, 10, 15	4.3	189	43.9
Quaking aspen (upland)	50, 60	12.3	286	23.3
Willow (lowland)	5, 5, 15, 20	4.0	59	14.7
Paper birch (upland)	60, 130	15.6	228	14.6
Balsam poplar (lowland)	10, 50, 60	18.5	269	14.5
Mountain alder (upland)	130	4.0	31	7.8
White spruce (upland)	55, 135, 165, 180	18.3	133	7.3
Black spruce (upland)	57, 62, 130, 130	5.5	30	5.5

* A rough estimate of energy density (concentration) in the vegetation type

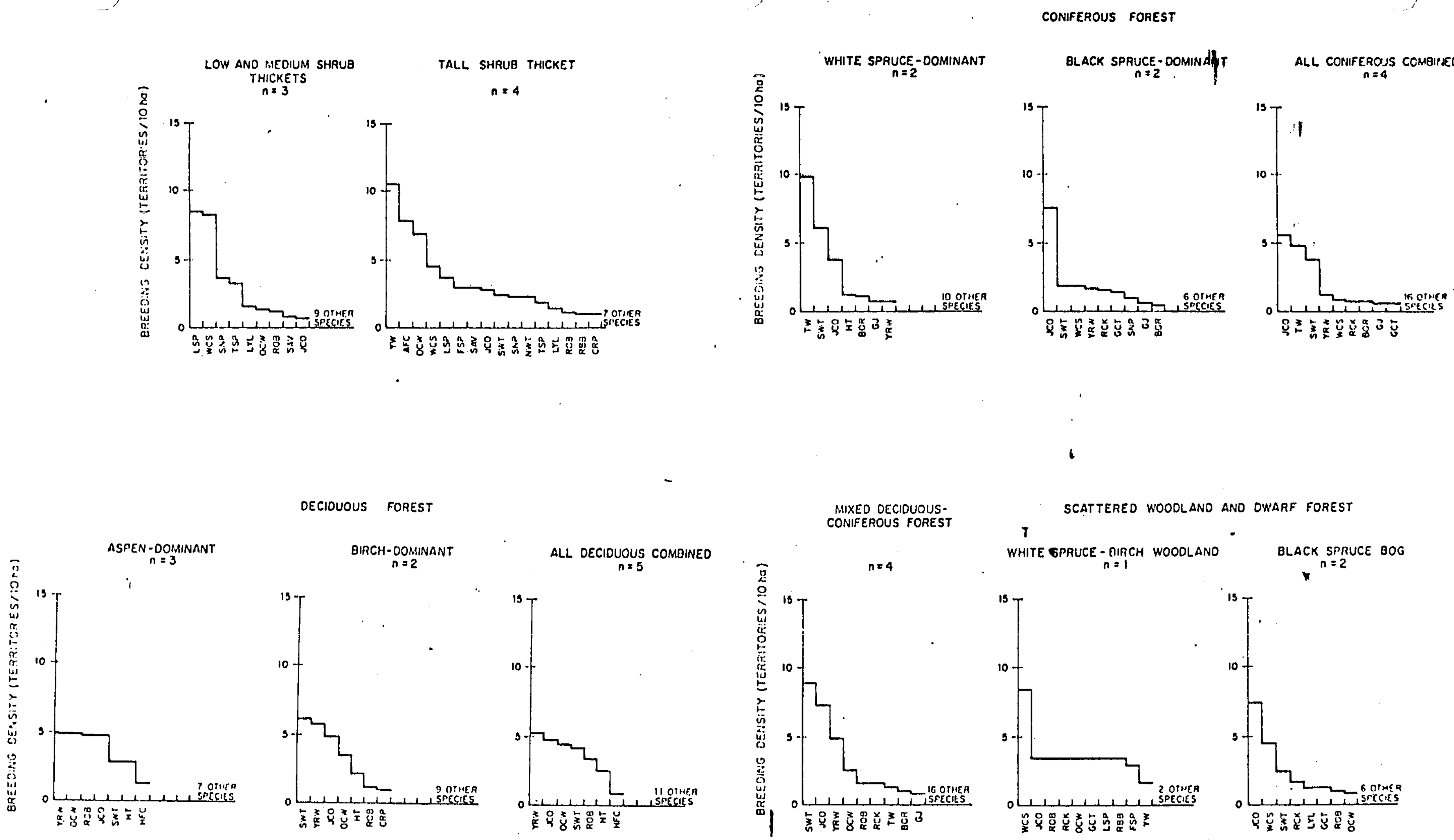

Figure 12. Bird species density-dominance structures for the ~~major woody~~ avian habitats of the Tanana River Valley, Alaska. Abbreviations for species are given in Table II.

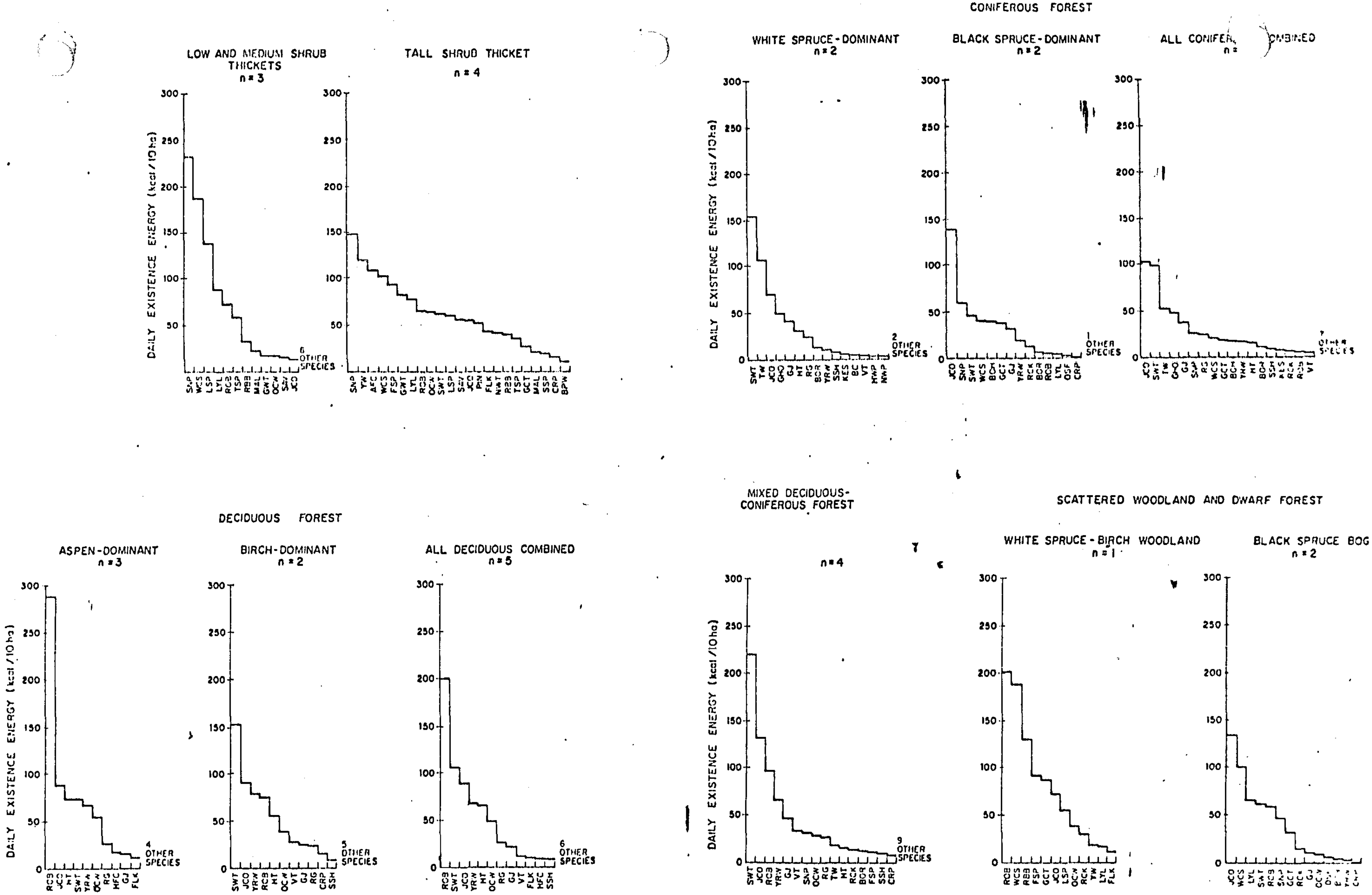

Figure 13. Bird species existence energy-dominance structure for the major woody avian habitats of the Tanana River Valley, Alaska. Abbreviations for species are given in Table II.

LE V

Partitioning of avian existence energy within avian habitats according to foraging guild, Tanana River Valley, Alaska.

Daily existence energy (M) is expressed in kcal/10 ha.

	EXISTENCE ENERGY (%)																	
	LOW AND MEDIUM SHRUB THICKETS		TALL SHRUB THICKET		DECIDUOUS FOREST				MIXED DECIDUOUS-CONIFEROUS FOREST		CONIFEROUS FOREST				SCATTERED WOODLAND AND DWARF FOREST			
					Aspen-dominant		Birch-dominant				White spruce-dominant		Black spruce-dominant		White Spruce-Birch Woodland		Black Spruce Bog	
FORAGING GUILD	(M)	(%)	(M)	(%)	(M)	(%)	(M)	(%)	(M)	(%)	(M)	(%)	(M)	(%)	(M)	(%)	(M)	(%)
Flycatchers	6	0.7	102	7.5	21	3.0	2	0.4	4	0.5	0	0	3	0.6	0	0	6	1.1
Foliage searchers	23	2.6	196	14.5	130	18.3	133	23.3	161	21.4	137	27.5	43	9.9	86	9.2	35	6.5
Timber gleaners	0	0	0	0	1	0.1	5	0.8	6	0.8	10	2.0	3	0.6	0	0	0	0
Timber drillers	0	0	0	0	0	0	0	0	0	0	9	1.8	3	0.8	0	0	0	0
Ground-brush foragers	510	57.3	633	46.7	559	78.6	378	66.6	545	72.2	282	56.5	331	75.8	834	89.0	393	73.1
Raptors	0	0	0	0	0	0	51	8.9	9	1.2	61	12.2	0	0	0	0	0	0
Aquatic foragers	351	39.4	424	31.3	0	0	0	0	29	3.9	0	0	54	12.3	17	1.8	104	19.3

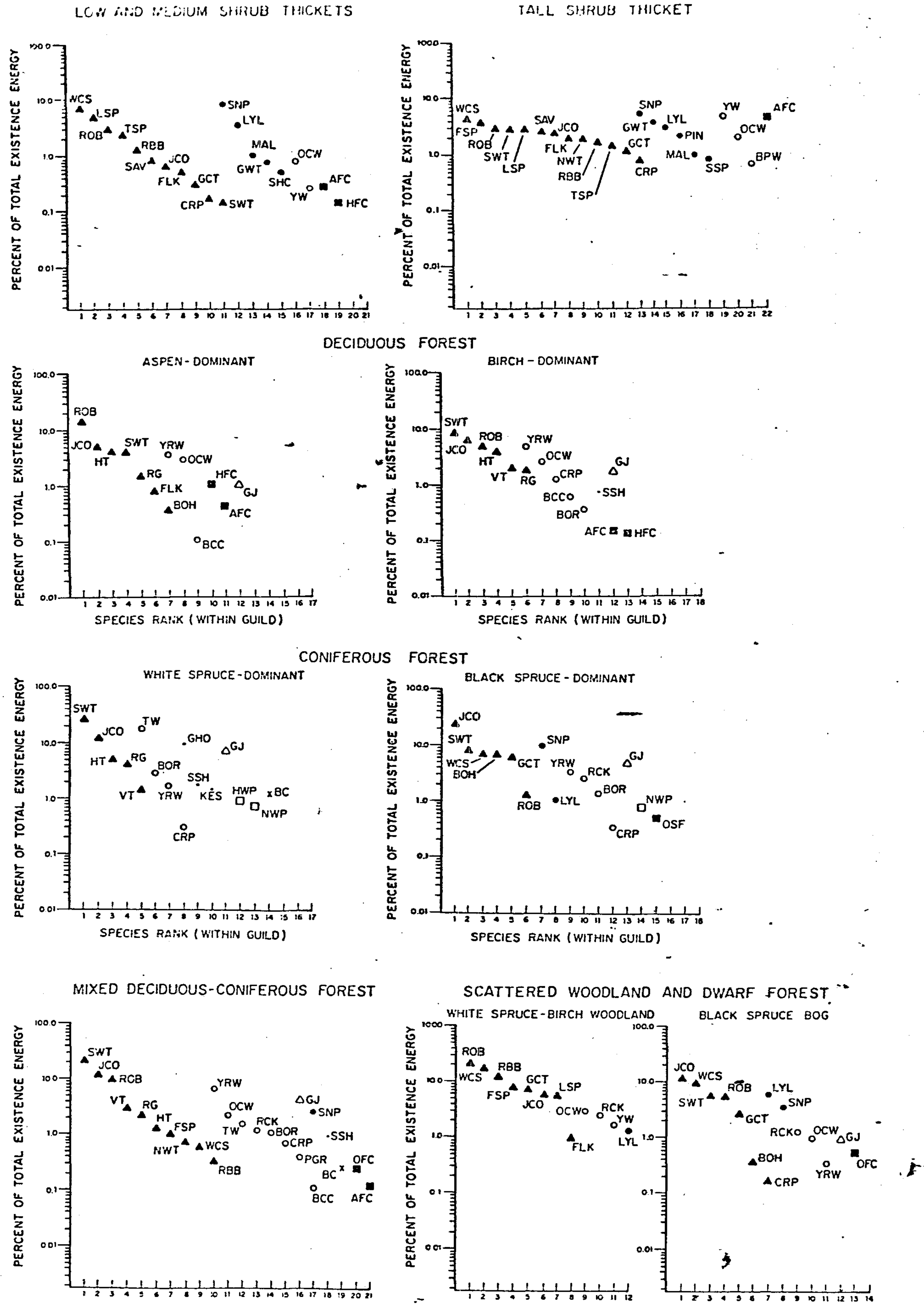

Figure 14. Existence energy-dominance curves for foraging guilds within the major woody avian habitats of the Tanana River Valley, Alaska. See Table II for species abbreviations. Key: ▲ = Ground-brush foragers, o = Foliage searchers, • = Aquatic foragers, × = Timber gleaners, □ = Timber drillers, ⊡ = Flycatchers, · = Raptors, Δ = Multiple guild (Gray Jay).

the more likely it will exhibit sigmoid dominance curves. In spite of the fact that only a few foraging guilds in the upper Tanana River Valley were large enough to illustrate curves (ground-brush foragers, foliage-searchers, and aquatic foragers), a range of resource division patterns was visible, and the patterns differed within the same foraging guild in different habitats.

Breeding Bird Communities

Low and Medium Shrub Thickets

Low and Medium Shrub Thickets were low in species richness and low to intermediate in levels of estimated biomass and existence energy, unless standing water was present, as in LMS1 (Table III). With water, LMS1 had twice the richness and three times the estimated biomass of otherwise similar LMS3. The habitat was dominated by Lincoln's Sparrow and White-crowned Sparrow, which together comprised over half of the total density (Fig. 12). These species, plus Common Snipe, Tree Sparrow, and Lesser Yellowlegs reached their greatest abundance in this habitat.

Ground-brush foragers and aquatic foragers (when water was present) dominated this habitat, with White-crowned Sparrow and Lincoln's Sparrow dominating the existence energy by the former guild and Common Snipe and Lesser Yellowlegs, the latter. The existence energy-dominance curves were essentially straight (Fig. 14), suggesting niche pre-emption in the ground-brush forager guild and few species, probably niche-isolated, in the other guilds.

Tall Shrub Thicket

Tall Shrub Thickets supported the highest species richness and occupancy levels of any avian habitat in the Tanana River Valley, supporting up to 18 breeding species and densities as high as 67.7 territories per 10 ha (Table III). The most abundant species were Yellow Warbler, Alder Flycatcher, and Orange-crowned Warbler. These species, plus Northern Waterthrush, Blackpoll Warbler, Fox Sparrow, and Savannah Sparrow, reached their greatest abundance in Tall Shrub Thickets (although the Savannah Sparrow densities appear to be an aberration caused by edge effect on 1.6 ha-miniplot TS2, adjacent to the Northway airport). The density-dominance structure was the most even observed (see Fig. 12). The Tall Shrub Thickets also had the greatest estimated daily existence energy (up to 1968 kcal/10 ha; average 1355 kcal/10 ha), 52% higher than the next highest habitat.

Four foraging guilds were represented in this habitat, and three (aquatic foragers, foliage searchers, and flycatchers) attained their greatest existence energy here ("M" in Table VIII). The dominant guild, the ground-brush foragers, accounted for almost half of the total existence energy, aquatic foragers almost a third. The four highest energy users of the habitat (Common Snipe, Yellow Warbler, Alder Flycatcher, and White-crowned Sparrow) each represented one of the four major guilds. The existence energy-dominance curve for the ground-brush foraging guild was sigmoid in shape and horizontal, indicating a high species diversity, with little competitive advantage among a number of intermediate-abundance species. The curve for the aquatic foragers was also sigmoid, but steeper. The steep, straight line formed by the three foliage searchers suggests niche pre-emption, even though the data points were few.

Deciduous Forest

Deciduous Forests, in general, supported intermediate breeding densities and numbers of species. Total breeding density and the density of certain bird species (e.g., Dark-eyed Junco, Yellow-rumped Warbler, and Orange-crowned Warbler) were remarkably consistent among plots sampled within this habitat. Species richness, species composition, density-dominance structure, and patterns of resource division of the two major vegetative types within this habitat, however, were quite different. Aspen-dominant stands supported greater biomass and had higher existence energy estimates, but had fewer species than birch-dominant stands. As with all other habitats, ground-brush foragers dominated the energetic relationships; and existence energy-dominance curves for all guilds were relatively straight, suggesting niche isolation among few species in those guilds with sufficient data points.

In aspen stands, Yellow-rumped Warbler, Orange-crowned Warbler, American Robin, and Dark-eyed Junco were the most abundant species, comprising 70% of total density. American Robin, Hermit Thrush, and Hammond's Flycatcher reached their greatest abundance in aspen stands. The density-dominance structure was unique, with the four most abundant species having nearly equal densities (Fig. 12). The existence energy-dominance structure (Fig. 13), on the other hand, was overwhelmingly dominated by a single species, American Robin.

In birch stands, the most abundant species was the Swainson's Thrush. This species, plus the next three most abundant ones--Yellow-rumped Warbler, Dark-eyed Junco, and Orange-crowned Warbler--comprised 77% of total density. The Yellow-rumped Warbler and Black-capped Chickadee reached their greatest abundance in birch stands. The density-dominance structure was characteristic of a diverse community, with an even, gradual decline in species abundance across the graph (Fig. 12). Swainson's Thrush and Dark-eyed Junco dominated the ground-brush forager guild. Raptors were well represented with breeding Sharp-shinned Hawks and Great Horned Owls.

Mixed Deciduous-Coniferous Forest

Of all the forest habitats, Mixed Deciduous-Coniferous Forest supported the largest number of species, the highest breeding density and biomass, and the greatest existence energy in the Tanana River Valley. The most abundant species were Swainson's Thrush and Dark-eyed Junco, which together comprised 48% of the breeding density; the Yellow-rumped Warbler was also numerous. Swainson's Thrush and Varied Thrush reached their greatest abundance in the Mixed Deciduous-Coniferous Forest habitat, and this was the only habitat in which breeding Pine Grosbeaks were found. Large numbers of apparently non-breeding Common Redpolls and White-winged Crossbills used this habitat extensively. Both the density-dominance structure and the foraging guild curves were characteristic of diverse communities, the former showing an even, gradual decline in species abundance across the graph (Fig. 12) and the latter, a sigmoid-shaped curve for the two dominant foraging guilds--ground-brush foragers and foliage searchers (Fig. 14).

The combination of deciduous and coniferous life forms provided a diverse habitat structure, which was used by six foraging guilds. Ground-brush foragers and foliage searchers dominated existence energy, with three ground-brush foragers--Swainson's Thrush, Dark-eyed Junco, and American Robin--using over half (56%) of the total avian existence energy.

One 1.6-ha Mixed Forest miniplot, the Upland White Spruce-Sapling Birch (MF5), was excluded from the summary of population data (Table III) because of its unexplained, aberrantly low density; there was no evidence of breeding birds on this plot.

Coniferous Forest

Coniferous Forests generally had the lowest occupancy levels of the forest habitats, supporting the lowest breeding density and biomass, the fewest species, and having the lowest estimated existence energy of any of the habitats. The most abundant breeding species were Dark-eyed Junco, Townsend's Warbler (white spruce only), and Swainson's Thrush, which together comprised 67% of the breeding density. Dark-eyed Junco and Swainson's Thrush, both ground-brush foragers, also overwhelmingly dominated total existence energy.

The two major vegetation types within this habitat--white spruce-dominant stands and black spruce-dominant stands--had considerably different numbers of species, breeding densities, and density-dominance structures, with the black spruce stands less diverse and with lower occupancy levels than comparably-located (upland/lowland) white spruce stands.

In white spruce stands, the Townsend's Warbler, a recent colonizer in interior Alaska (Kessel and Springer 1966), was the most abundant bird; this species, together with the next most abundant ones--Swainson's Thrush and Dark-eyed Junco--comprised 82% of total density. Townsend's Warbler, Brown Creeper, and Boreal Chickadee reached their greatest abundance in white spruce stands. Large numbers of White-winged Crossbills, Bohemian Waxwings, Pine Siskins, and Common Redpolls, which were apparently non-breeders, used white spruce stands extensively during the breeding season. Breeding species richness was low, with an uneven distribution of species abundance and high dominance by the three most abundant species (Fig. 12). The existence-energy-dominance curves of the major foraging guilds were essentially straight, probably because of the few species in each guild having widely-separated niches (Fig. 14).

Three foraging guilds reached their maximum existence energy in white spruce stands: raptors (Sharp-shinned Hawk, American Kestrel, and Great Horned Owl), timber gleaners (Boreal Chickadee, Brown Creeper), and timber drillers (Hairy Woodpecker and Northern Three-toed Woodpecker). Foliage searchers reached their maximum dominance (28%) in this vegetation type, apparently because of the deep, extensive, and vertically-incised canopy characteristic of climax white spruce stands. Ground-brush foragers, however, dominated total existence energy here as in all the other habitats.

A single species, Dark-eyed Junco, dominated the black spruce stands and comprised 40% of the total breeding density. This dominance caused a unique community density-dominance structure, with one dominant species and an even distribution of the remaining, less common species (Fig. 12).

Ground-brush foragers dominated total estimated existence energy in black spruce stands, with lesser proportions in aquatic foragers and foliage searchers. The presence of the aquatic foraging guild was possible because of wet areas within black spruce stands undergoing paludification. The existence energy-dominance curve for the ground-brush foragers was sigmoid in shape, while that of the foliage searchers resembled that for the white spruce stands.

Scattered Woodland and Dwarf Forest

Scattered Woodland and Dwarf Forest was represented by two distinct vegetation types: White Spruce-Birch Woodland and Black Spruce Bog. These types tended to correspond with their nearest forest counterparts (Mixed Deciduous-Coniferous Forest for Woodland and black spruce stands for Dwarf Forest) in community characteristics, except that they supported higher breeding densities and had greater existence energies. Dark-eyed Junco and White-crowned Sparrow were the most abundant species and comprised 45% of total breeding density. Less abundant breeding species found in both types were, in decreasing order of abundance, Ruby-crowned Kinglet, Gray-cheeked Thrush, American Robin, and Orange-crowned Warbler. Ruby-crowned Kinglet and Gray-cheeked Thrush reached their greatest abundance in this habitat.

The White Spruce-Birch Woodland had a much greater species richness, breeding density, and existence energy than Black Spruce Bog. The relatively high number of species was made possible by the combination of coniferous and deciduous life forms with that of shrub thickets. White-crowned Sparrow was the most abundant species, comprising 21% of the breeding density. The presence of one dominant species and several equally-abundant species of intermediate density (Fig. 12) resulted in a density-dominance structure similar to that of black spruce stands. Ground-brush foragers reached their maximum dominance in the White Spruce-Birch Woodland, using 89% of total existence energy. The existence energy dominance curve for the ground-brush foraging guild was a horizontal, sigmoid curve, typical of diverse communities.

Black Spruce Bogs, paralleling black spruce stands, had a low number of species and low occupancy levels (Table III). Dark-eyed Junco and White-crowned Sparrow were the most abundant species, comprising 60% of total breeding density. No birds achieved their greatest abundance in this Dwarf Forest. The density-dominance structure showed a dominance of two species and a gradual decline in abundance of species of intermediate density. Ground-brush foragers dominated total existence energy; their existence energy-dominance curve was sigmoid.

Permanent Resident Birds

Permanent resident species on the census plots generally occurred in much lower densities than migrant species. Estimation of density by territory mapping was inappropriate for many of these species; some initiated breeding activities 1 to 3 months before we started our censuses (Great Horned Owl, Gray Jay, chickadees, and White-winged Crossbill) and others were non-territorial or tended to aggregate (Bohemian Waxwing and Common Redpoll). Therefore, we used the mean number of individuals observed per census as an index to compare abundance of permanent resident species (Table VI). In contrast to the pattern observed for breeding density, the habitats containing coniferous trees supported the highest number of species and greatest densities of permanent residents (contra Willson 1976; 10.7% of breeding bird density in coniferous forests consisted of permanent residents, compared to 4.1% of deciduous forest breeding bird density). White spruce-dominant forests supported the greatest number of species and greatest density of permanent residents; black spruce-dominant forests and Mixed Deciduous-Coniferous Forests supported intermediate densities; Deciduous Forests and Tall Shrub Thickets supported low densities; and Low and Medium Shrub Thickets and Scattered Woodlands and Dwarf Forests supported minimal densities. Boreal Chickadee, Gray Jay, White-winged Crossbill, Great Horned Owl, and Spruce Grouse were most abundant in Coniferous Forests; Ruffed Grouse were most abundant in Mixed Deciduous-Coniferous Forests; Black-capped Chickadee was most abundant in Deciduous Forests; and Common Redpoll was most abundant in Tall Shrub Thickets.

T[illegible] VI

Comparison of abundance of permanent resident breeding bird species among the avian habitats, Tanana River Valley, Alaska, 1975 and 1977. Number of plots and sample area are the same as Table II. Figures are the mean number of individuals observed per 10 ha, per census. Numerals in parentheses indicate the number of plots in which the species occurred. A "+" denotes breeding in very small numbers.

SPECIES	LOW AND MEDIUM SHRUB THICKETS	TALL SHRUB THICKET	DECIDUOUS FOREST			MIXED DECIDUOUS-CONIFEROUS FOREST
			Aspen-dominant	Birch-dominant	All deciduous combined	
Spruce Grouse						
Ruffed Grouse			0.3 (1)	0.1 (1)	0.1 (2)	0.7 (1)
Great Horned Owl				1.1 (1)	0.4 (1)	
Hawk Owl	+ (1)	+ (1)				
Hairy Woodpecker						
N. Three-toed Woodpecker						
Gray Jay		0.7 (3)	2.4 (2)	1.2 (2)	1.9 (4)	3.7 (4)
Black-capped Chickadee		0.1 (1)	1.0 (3)	1.0 (1)	1.0 (4)	+ (1)
Boreal Chickadee		0.5 (3)	0.1 (1)	0.3 (1)	0.2 (2)	4.3 (4)
Bohemian Waxwing	1.3 (3)	0.1 (2)	1.4 (1)		0.9 (1)	0.4 (2)
Pine Grosbeak	0.2 (2)	0.5 (2)	0.2 (1)	+ (1)	0.1 (2)	0.3 (2)
Common Redpoll	1.4 (3)	3.1 (3)	1.0 (1)	1.2 (1)	1.1 (2)	1.8 (3)
White-winged Crossbill		0.5 (1)				1.8 (1)
TOTAL INDIVIDUALS	2.9	5.5	6.4	4.9	5.7	13.0
TOTAL NUMBER OF SPECIES	4	8	7	7	8	8

Continued

SPECIES	CONIFEROUS FOREST			SCATTERED WOODLAND AND DWARF FOREST	
	White spruce-dominant	Black spruce-dominant	All coniferous combined	White Spruce-Birch Woodland	Black Spruce Bog
Spruce Grouse		2.0 (1)	1.0 (1)		
Ruffed Grouse	0.2 (1)	0.4 (1)	0.3 (2)		
Great Horned Owl	2.2 (2)		1.1 (2)		
Hawk Owl					
Hairy Woodpecker	0.3 (1)		0.1 (1)		
N. Three-toed Woodpecker	0.4 (1)	0.8 (1)	0.6 (2)		
Gray Jay	3.8 (2)	4.6 (2)	4.2 (4)	0.4 (1)	3.0 (2)
Boreal Chickadee	10.0 (2)	2.0 (1)	6.0 (3)		
Bohemian Waxwing	0.3 (1)	1.0 (1)	0.9 (2)	0.9 (1)	0.2 (1)
Pine Grosbeak	+ (1)		+ (1)		
Common Redpoll	1.3 (1)	1.2 (1)	1.2 (2)		0.4 (1)
White-winged Crossbill	5.3 (2)	0.8 (1)	3.0 (3)		
TOTAL INDIVIDUALS	23.8	12.8	18.4	1.3	3.6
TOTAL NUMBER OF SPECIES	10	7	11	2	3

Annual Variation

To determine the magnitude of annual variation of avian populations in the upper Tanana Valley, we compared numbers of common breeding passerine species between 1971 and 1977 obtained by Kessel from roadside counts through typical interior Alaska vegetation types near Fairbanks. Annual mean numbers of total individuals per count varied a maximum of 26% over the seven years, while the maximum deviation from the mean for any one year was 17%. Annual variation in individual species differed considerably among species; generally, the most abundant species varied the least. Swainson's Thrush varied a maximum of 52% over the seven years, although the greatest departure from the mean of any one year was only 28%. Other common species that showed relatively small annual variation were Yellow Warbler, White-crowned Sparrow, Fox Sparrow, Northern Waterthrush, and American Robin. The less abundant species showed considerably more variation: Dark-eyed Junco, 126%; Ruby-crowned Kinglet, 121%; Varied Thrush, 100%; Yellow-rumped Warbler, 94%; and Wilson's Warbler, 79%.

The low but variable abundance of Dark-eyed Junco here contrasts markedly with its high abundance in forest habitats at Fairbanks in 1975 and in the Tetlin-Northway area in 1977. In fact, abundance of this species in the Fairbanks area was increasing during this period (pers. obs.).

The inverse relationship between abundance and annual variation (Fig. 15) was significant, both in linear regression ($y = 32.59 - 0.415x$, $R^2 = 0.433$, $n = 14$, $p < 0.02$) and in Spearman's rank correlation (Steel and Torrie 1960) ($r_s = 0.80$, $n = 14$, $p < 0.001$).

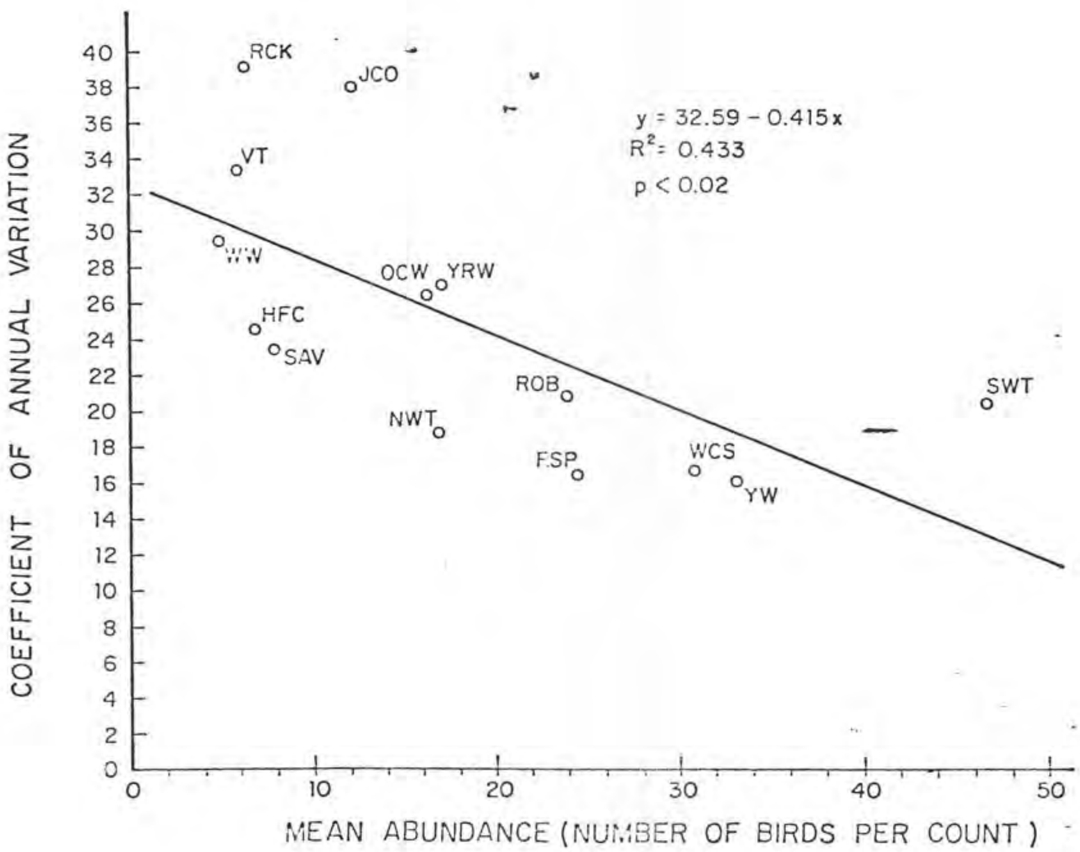

Figure 15. Inverse relationship between abundance and annual variation in 14 common migratory passerines during the breeding season, Fairbanks, Alaska, 1971-1977, based on roadside counts. See Table II for species abbreviations.

SPECIES HABITAT USAGE

Analyses of the measured habitat variables, combined with field observations on the height and activity of birds seen and the vegetation used, provided quantitative data with which to describe habitat use by the different bird species.

Vegetation and structural habitat variables are by nature interrelated (James 1971). Such correlations must be examined to adequately understand the patterns of habitat use. A correlation matrix of habitat variables in our study showed that 60% of the correlation coefficients were highly significant ($r > 0.321$, $n = 331$, $p < 0.001$). Most of the higher correlations illustrated the interdependence between forest growth and understory, topography and vegetation stature, and spatial arrangement of stems and canopy characteristics. Distance between trees, stem diameter, height, and canopy thickness indicated dominance of forest growth. Dominance of forest growth influenced light levels reaching the ground and hence influenced the type and vigor of ground and shrub cover. Some specific correlations prevalent throughout the species habitat analyses were litter ground cover and deciduous tree growth, moss ground cover and coniferous tree growth, thinleaf alder and water or openness, and inversely, forest growth variables with shrub or open habitat variables.

When analyzing for bird habitat selection through comparison of statistically selected habitat variables, one must assume that predictable relationships exist between the occurrence of a bird and its characteristic vegetational requirements (James 1971). The correlation of the presence or absence of a variable (or a certain value of that variable) with a species presence or absence, however, does not necessarily indicate a causal relationship. Also, habitat selection by a species is undoubtedly influenced by a number of interrelated variables combining to form the "niche-gestalt" of James (1971).

Some habitat variables in this study were not distributed in a normal pattern over all habitats, resulting in some sampling artifacts; this problem was particularly true of woody plant species composition. As a result, for example, statistical analyses frequently selected thinleaf alder as important for any of the shrub birds that occurred in any numbers on TS1, which had a relative importance value for this alder of 36.6%--the only plot in which its importance value was other than zero. Similar aberrations occurred relative to balsam poplar and shrub thicket birds, and black spruce and some Coniferous Forest birds. With tall shrub birds, analysis of variance (ANOVA) indicated a selection for openness as measured by distance between trees, whereas multiple regression (REGRN) often indicated a negative correlation with that variable--an ambivalence caused by the fact that most tall shrub thickets have some stems greater than 5 m high. Also, because mean values of measured variables for Deciduous Forests nearly coincided with the means of the range of all habitats, ANOVA, which was based on a comparison of means of species-present and species-absent subplots, often failed to show significant differences for Deciduous Forest birds.

When interpreting the results of ANOVA, REGRN, and discriminant function analysis (DFA), it was important to limit consideration of relationships and habitat use patterns to those of high statistical significance, preferrably $p < 0.001$. Use of lower significance levels resulted in the inclusion of "artifacts" in the described habitat use patterns. Generally, we found positive correlations more helpful than negative ones in defining habitat use.

In the following species accounts, habitat variables that were shown by statistical analyses to be significant habitat characteristics are discussed first; this information is then supplemented by data from field observations. Bird height observations are followed by standard deviations. Specific data used in these analyses and discussions are from the 331 subplots of the 1977 study, although, where helpful, reference is made to Spindler's (1976) study near Fairbanks in 1975.

Shrub Thickets

Eight bird species in the upper Tanana River Valley showed a primary preference for open, largely treeless habitats (Table VII). These open habitats concomitantly supported shrubbery of varying densities and heights. The major bases for partitioning of shrub habitats among species appeared to be height of shrubs and openness.

Alder Flycatcher favored shrub habitats in which mean brush densities were higher than for any other bird species (Table VII). Additionally, flycatcher densities were greatest (9.6-10.5 territories/10 ha) in habitats with a high density of stems in the tall shrub layer, i.e., the

TABLE VII

Mean values of variables which best distinguished the habitats of birds of the shrub thickets, upper Tanana River Valley, Alaska, 1977. Values are from species-present subplots and are followed by standard deviations.

Species	No. of subplots	Water (% ground cover)	Edge (0-1)	Distance between stems ≥ 25.4 mm (m)	Distance between trees (m)	Stem height (m)	Total canopy coverage (%)	Brush density @ 1 m (stems x 10^3/ha)	Stem heterogeneity index
Tree Sparrow	21	1±2	0.38±0.12	14.1±11.1	51.9±27.8	3.4±0.7	7±14	25.47±25.50	78.5
Savannah Sparrow	15	2±4	0.67±0.25*	19.9±16.3	48.4±38.6	3.8±0.9*	10±11	26.10±19.41	81.5
Lincoln's Sparrow	49	5±9	0.55±0.19	14.6±13.6	42.0±33.2	3.7±0.8	14±22	27.09±24.05	93.0
White-crowned Sparrow	52	2±5	0.67±0.24	13.2±13.0	38.3±31.9	3.7±0.8	11±18	24.48±23.06	98.7
Rusty Blackbird	30	6±13	0.53±0.18	8.8±10.6	25.8±25.3	4.0±1.1	17±28	22.39±19.66	121.1
Yellow Warbler	34	3±7	0.50±0.17	5.6±9.1	14.5±19.0	4.6±2.1	34±31	32.96±27.89	162.7
Fox Sparrow	22	3±7	0.55±0.19	6.0±10.5	12.6±20.5	4.3±0.8	36±30	36.61±26.74	56.5
Alder Flycatcher	27	1±2	0.67±0.24	3.7±2.7	12.8±17.1	5.6±3.3	44±29	39.38±30.66	72.5

*Height and edge biased by high density of Savannah Sparrows at edge of Tall Shrub Thicket (TS2)

Tall Shrub Thickets--although a few territories occurred in habitats that did not attain tall shrub height. Fifty-six percent of the birds observed were at tree heights, whereas 37% were below 2.5 m--half in medium and half in low shrubs. The Alder Flycatcher apparently used the lower layers of vegetation for nesting (see Stein 1958), but used the taller shrubs for song perches and for foraging. Forty-three percent of birds observed were in willow, whereas only 12% each were in alder and poplar. Habitats supporting Alder Flycatchers were mostly flat or gently sloping, often poorly drained with some exposed surface water ($p < 0.017$, REGRN), and usually had significant amounts of sedge-grass ground cover (mean of 21%; $p < 0.019$, REGRN). Avoidance of forest characteristics was evident.

Yellow Warbler clearly selected tall shrub thickets.—It occurred on most of the same plots as the Fox Sparrow (see below), and most of the measured habitat values were similar--including high values for brush and foliage volume in the low shrub layer, a high percentage of stem density in the tall shrub layer, and a general avoidance of closed forest characteristics. Yellow Warbler behavior differed from the Fox Sparrow, however, in that the warbler made little use of the low shrub layer; 48% of birds were observed in the tall shrub layer, 31% in the medium shrub layer, and 17% in the tree layer. The index of stem heterogeneity in Yellow Warbler subplots was high, which, in shrub habitats, means open patches within the thickets. Seventy-one percent of Yellow Warblers observed were in willow; 8% each were in poplar and white spruce, and only 6% in alder. ANOVA in this study, as well as in an earlier one by Spindler (1976), showed that the presence of water was important ($p < 0.001$); and certainly, in general, this bird is most abundant in lowland and riparian situations in interior Alaska.

Rusty Blackbird favored open habitats with water ($p < 0.001$, DFA; mean habitat value for water was higher than for any other shrub thicket bird); and it showed a preference for tall shrubs (mean habitat value of 68% stems in tall shrub layer; $p < 0.001$, ANOVA). Observations showed 36% in white spruce, 30% in willow, and only 10-12% each in alder, poplar, and dead snags. Heights of birds observed were somewhat distorted by the habit of disturbed Rusty Blackbirds to seek high perches; 62% were recorded in the tree layer, 21% in the tall shrub layer, and 12% in the medium shrub layer.

Savannah Sparrow was second only to the Tree Sparrow in its obvious preference for open habitats (Table VII). Its presence corresponded with a high proportion of foliage volume in the low shrub layer (76%; $p < 0.008$, REGRN), but there was no significant correlation for any particular type of ground cover. Because one of the areas of high Savannah Sparrow density was at the edge of a tall shrub thicket (TS2), which birds used for song perches, habitat statistics overemphasized the importance of the density of the taller shrub stems (see Fig. 17). Observations, many of singing birds on song perches, showed 26% of activity below 1.2 m, 52% in the medium shrub layer, and 18% in the tall shrub layer; 76% of birds observed were in willow.

The Tree Sparrow showed a clear preference for open habitats; 23% of variation in abundance was explained by distance between trees ($p < 0.003$, REGRN). Species-present subplots had less canopy coverage than for any other bird species; and, conversely, the distance between trees was greater than for any other species (Table VII). In spite of the openness, there was no evidence of any ground cover preference. Ninety-three percent of the birds observed were in shrubs <2.5 m high--67% in the medium shrub layer, including many on song perches; 80% of observed activity was in willow.

White-crowned Sparrow habitat statistics emphasized avoidance of forest and tall shrub habitats and selection of open, low-medium-height shrubbery ($p < 0.001$, ANOVA). Forty percent of variation in abundance was explained by low canopy coverage ($p < 0.005$, REGRN); only Tree and Savannah sparrow habitats had lower canopy coverage or greater distance between trees (Table VII). Direct observations showed 39% of activity below 1.2 m and 38% in the medium shrub layer; 43% of White-crowned Sparrows observed were in willow, 26% in white spruce, and 26% either on the ground or on dead branches.

Fox Sparrow favored tall shrub thickets with growth particularly dense in the layer below 1.2 m (proportion of foliage volume in low shrub layer, $p < 0.003$, REGRN, and brush, $p < 0.001$, REGRN and DFA). Brush density was second only to the Alder Flycatcher (Table VII), and the greatest foliage volume (43%) was in the low shrub layer. There was a predominance of stems in the tall shrub layer (60%). Paralleling this habitat structure was a dichotomy in use by the Fox Sparrow; 62% of observed activity was actually at tree heights, mostly males singing from prominent perches, whereas 31% was below 1.2 m, where they did most of their foraging. Observations showed 38% of birds on White Spruce, 31% on the ground, and 19% in dead shrubs. Fox Sparrow was the only species that showed even a suggestion of a positive response to the presence of forb ground cover ($p < 0.05$, ANOVA). The Fox Sparrow data showed avoidance of closed forest features, although some Fox Sparrow in interior Alaska nest in open deciduous forests where there is a dense understory of tall willows and low brush, usually along draws or in openings.

Lincoln's Sparrow exhibited a strong selection for open habitat; 53% of variation in abundance was accounted for by the single variable distance between trees ($p < 0.001$, REGRN). Structurally, its habitat was quite similar to that of the White-crowned Sparrow (Table VII), but Lincoln's Sparrow differed in its possible preference for damp habitats with water, sedge-grass ground cover, and high brush density ($p < 0.007$, REGRN). Fifty percent of Lincoln's Sparrow observed were in the low shrub layer--compared to only 39% in White-crowned Sparrow--and 29% were in the medium shrub layer. Seventy-five percent of birds observed were in willow and 16% on dead shrubs.

Deciduous Forests

Four species of birds showed a primary preference for Deciduous Forests or for the deciduous tree component of Mixed Deciduous-Coniferous Forests (Table VIII).

TABLE VIII

Mean values of variables which best distinguished the habitats of birds of Deciduous Forest and of Mixed Deciduous-Coniferous Forest, upper Tanana River Valley, Alaska, 1977. Values are from species-present subplots and are followed by standard deviations.

Species	No. of subplots	Edge (0-1)	Stem diameter (mm)	Distance between trees (m)	Stem height (m)	Total canopy coverage (%)	Relative importance value (%)			Tree heterogeneity index
							Birch	Aspen	White spruce	
Hammond's Flycatcher	13	0.54±0.19	110±30	5.2±8.1	10.6±3.3	68±22	22	34	6	154.3
Black-capped Chickadee	17	0.29±0.08	120±40	2.8±0.7	10.4±2.8	79± 7	38	21	6	25.8
Hermit Thrush	35	0.51±0.17	130±40	2.9±1.0	11.0±3.3	75±11	24	29	14	34.1
Yellow-rumped Warbler	147	0.19±0.04	120±50	3.1±1.7	11.0±3.3	74±14	29	22	22	53.1
Varied Thrush	47	0.00	130±40	3.3±1.2	10.2±3.7	73±20	34	5	30	34.1
Swainson's Thrush	212	0.18±0.04	120±50	3.9±5.5	10.7±4.0	68±20	23	14	33	142.5
Dark-eyed Junco	198	0.21±0.05	120±50	4.0±5.4	10.4±4.0	67±22	25	16	29	134.6

Hammond's Flycatcher territories occurred only on Deciduous Forest plots. Only 8% of the variation in abundance was explained by the measured habitat variables, largely because only four territories or parts of territories were on the study plots. Nonetheless, statistics indicated a preference for poplar-aspen forests, and mean habitat values for species-present subplots showed a preference for tall, well-developed deciduous forests (Table VIII). Compared to the other predominantly mature deciduous forest species--Black-capped Chickadee, Hermit Thrush, and Yellow-rumped Warbler--the habitat of the Hammond's Flycatcher was more heterogeneous and a bit more open (Table VIII). Although this species nests in both paper birch and quaking aspen forests in interior Alaska, this study revealed a possible preference for aspen, a habitat that Swarth (1922, 1924) found them favoring in the Skeena and Stikine river valleys of British Columbia. Observations showed 62% of activity in aspen (even though mean aspen relative importance value was only 34%), 15% in birch (relative importance value, 22%), but none in spruce; 72% of activity was in the tree stratum (mean height, 6.5 $\pm$ 3.0 m).

Black-capped Chickadee showed as strong a selection for Deciduous Forests (combined deciduous tree importance, 61%) as the Boreal Chickadee did for Coniferous Forests (Fig. 16) and, like its congener, it favored spatially homogeneous forests (lowest index of tree heterogeneity of any bird species in this study). Statistical treatments of the habitat variables showed little, except avoidance of white spruce ($p < 0.001$, REGRN), undoubtedly in part because only four territories or parts of territories were on the study plots. An examination of mean habitat

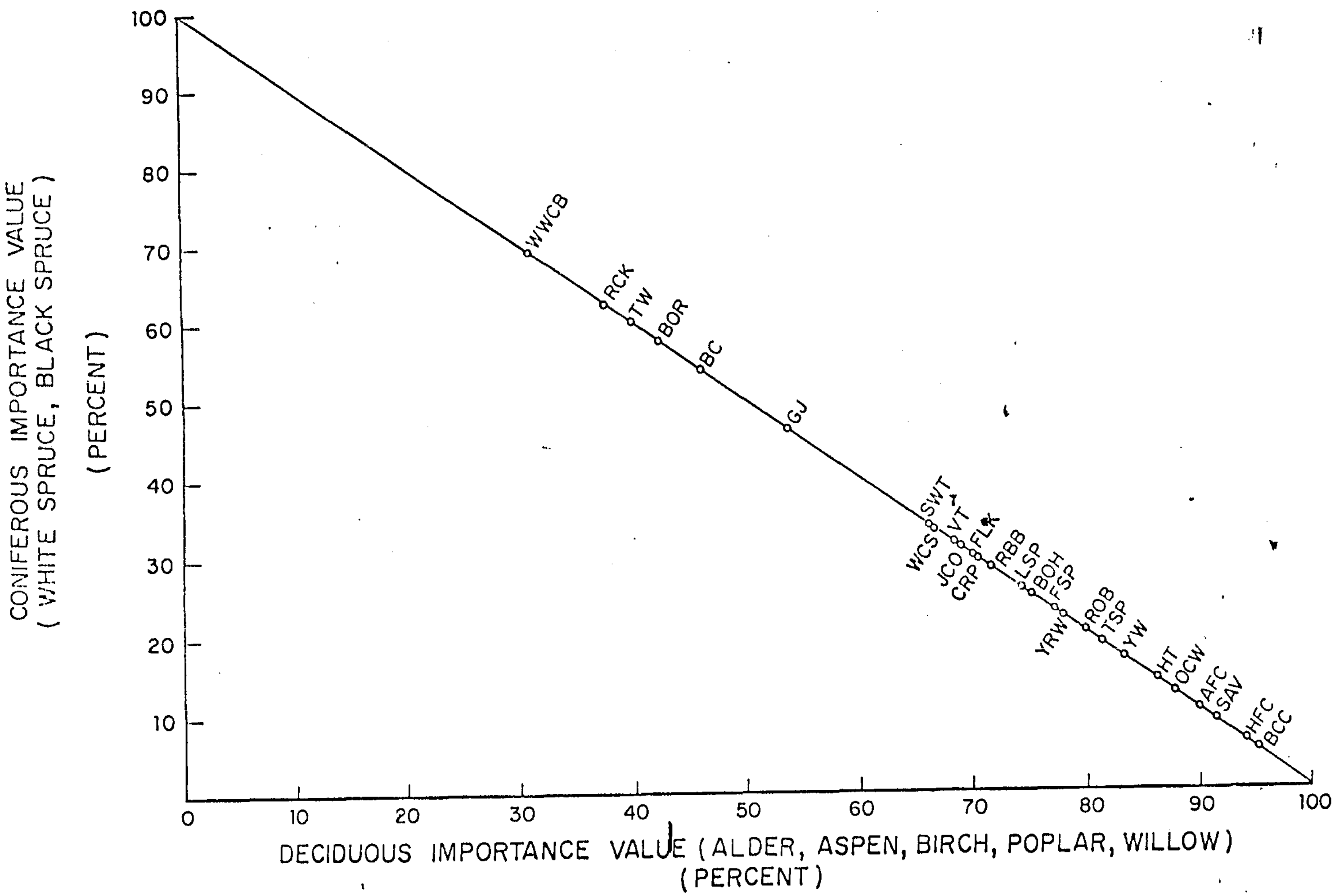

Figure 16. Ordination of 26 taiga birds on a gradient from pure coniferous to pure deciduous habitat in the upper Tanana River Valley, Alaska, based on mean habitat variables of importance values of coniferous trees vs deciduous trees and shrubs. See TableII for bird species abbreviations.

values for species-present subplots (Table VIII), however, showed a preference for relatively dense deciduous forests with large trees; total canopy coverage was greater than for any other bird species. Within Deciduous Forests, the Black-capped Chickadee showed some preference for paper birch; habitats had mean relative importance values of 38% for birch and 21% for aspen. Sixty percent of the birds were observed in birch, with 20% each in aspen and poplar; 92% were observed in the tree stratum (mean height, 7.1 ± 2.9 m).

Hermit Thrush habitat measurements, as those of most other deciduous forest birds, failed to show any useful variables with multiple regression. Mean habitat values of species-present subplots, however, showed a clear preference for mature, relatively dense deciduous forests (Table VIII). We found that territories almost invariably occurred at the edge of internal forest openings, such as blowdowns, powerlines, etc., a phenomenon described also by Dilger (1956), although the index of tree heterogeneity was low. Territories were present on all of the Deciduous Forest plots and on one mixed (MF1) and one coniferous (CF2) plot. There were some indications of a preference for quaking aspen stands: ANOVA showed a positive selection for aspen ($p < 0.005$); highest density of territories occurred on an aspen-dominant plot (DF3); and 29% of the birds observed were in aspen (46% were on the ground and 11% were in paper birch). In view of the apparent preference of Hermit Thrush farther east in North America for habitats with conifers (Dilger 1956, Godfrey 1966), it is noteworthy that our study showed avoidance of white spruce ($p < 0.001$, DFA). Hermit Thrush is primarily a ground nester and forager, and 52%

of the activity we observed was below 1.2 m; 29%, primarily singing males, was in the tree stratum.

Yellow-rumped Warbler favored forest habitats; 21% of variation in abundance was explained by a high proportion of foliage in the tree layer ($p < 0.001$, REGRN). It occurred on almost all of the forest plots, whether deciduous, mixed, or coniferous, but its densities were greatest in the deciduous and mixed forests. Mean habitat values (Table VIII) showed that it favored mature deciduous forests of either paper birch or quaking aspen. Species-present subplots had a combined deciduous tree importance value of 53%--29% birch, 22% aspen, and 2% poplar--and a white spruce importance of 22%. Both ANOVA and DFA indicated a possible avoidance of white spruce ($p < 0.005$). Observations showed 42% use of birch, 33% aspen, and 8% white spruce; 83% of activity was in the tree layer and 16% in the medium and tall shrub layers, where this warbler normally nests (mean height, 6.5 ± 2.8 m).

Mixed Deciduous-Coniferous Forests

Three species of birds appeared to prefer Mixed Deciduous-Coniferous Forests (Table VIII), although all used other habitats as well. The Varied Thrush appeared to select this habitat primarily because of the kind of dense understory it provided, whereas the widespread Swainson's Thrush and Dark-eyed Junco appeared to be abundant because of the juxtaposition of the two tree life forms.

Varied Thrush prefer shaded, relatively moist habitats of dense foliage (Gabrielson and Lincoln 1959, Godfrey 1966), characteristics that were not measured well by our habitat variables. These characteristics, however, were best met on our study area where the big-leaved, shade-tolerant mountain alder grew under a forest canopy and where spruce were present. Both ANOVA and DFA indicated selection for mountain alder and paper birch ($p < 0.001$) and ANOVA showed avoidance of edge ($p < 0.001$). Only seven territories or parts of territories occurred on the study plots, one in a birch deciduous forest, two partial territories in a white spruce forest, and the rest in Mixed Deciduous-Coniferous Forests. A forest canopy, however, is not a habitat requirement, per se, as Varied Thrush breed in Tall Shrub Thickets, primarily mountain alder, beyond treeline in western Alaska (Kessel, pers. obs.). Observations showed 42% of birds in birch, 25% on the ground, and 21% in white spruce, but none in alder. Sixty-four percent were in the tree layer and 27% were below 1.2 m (mean height, 5.4 ± 4.7 m).

Swainson's Thrush showed a preference for forest habitats (Table VIII), although it occurred on almost all of the study plots, except the most open ones (Low and Medium Shrub Thickets and Scattered Woodlands); it was second only to Dark-eyed Junco in overall abundance (84.3 territories on study area). Relatively high densities (>5 territories/10 ha) occurred on mature forest plots in which either white spruce or paper birch had high importance values, a species composition that, among other things, mitigated against a high ground cover of dwarf shrubs, which Swainson's Thrush tended to avoid ($p < 0.005$, DFA); deciduous forests with high importance values of aspen had higher percentages of dwarf shrub ground cover and lower numbers of Swainson's Thrush. Highest densities occurred on Mixed Deciduous-Coniferous Forest plots with low (<20%) dwarf shrub ground cover (10.8 and 11.0 territories/10 ha on MF1 and MF2, respectively). Multiple regression selected litter as an important variable ($p < 0.001$), which would seem logical on the basis of time spent foraging on the ground, but intercorrelations suggest that litter may have been first included in the regression equation based on its high value in all plots with high deciduous tree importance, i.e., all deciduous and mixed forest plots. About half of the foliage volume in Swainson's Thrush habitat was in the understory (49%) and the habitat had a fairly high spatial heterogeneity (Table VIII); coupled with these habitat characteristics, this bird, except when singing, carried out most of its nesting and maintenance activities in the understory. Observations showed 41% of activity in the tree layer, 36% below 1.2 m, and 17% in the tall shrub layer (mean height, 3.9 ± 3.8 m); 26% of birds observed were on the ground, 21% in aspen, 20% in birch, 12% in mountain alder, and 10% in white spruce.

Dark-eyed Junco showed a preference for forest and woodland habitats (Table VIII)--whether deciduous, mixed, or coniferous--although it also occurred in shrub thickets, especially tall shrubs. Junco was the most widespread and abundant breeder on the study area; it occurred on more of the plots than any other species (19 of 23 plots, excluding MF5) and there was a total of 106.5 territories, 25% more than for the next most abundant species, Swainson's Thrush. Statistical analyses failed to elucidate any meaningful habitat variables. Mean habitat values on species-present subplots, however, indicated a preference for forests, especially with fairly high tree heterogeneity (Table VIII). The junco did not appear to favor edges or forest openings as much as it apparently does farther east (Godfrey 1966, Eaton 1968). Primarily a bird of the understory, where it nests and forages on or near the ground, 47% of birds were observed below 2.5 m; an additional 10% were in the tall shrub layer, and 42% were in the tree layer (mean height, 3.4 ± 3.1 m). Twenty-four percent were in white spruce, 21% on the ground, and 11-33% each were in birch, aspen, and willow.

Coniferous Forests

Six species of birds showed a primary preference for habitats dominated by spruce (>50% relative dominance) (Table IX and Fig. 16), and they had breeding territories only in such habitats. Gray Jay and Ruby-crowned Kinglet preferred more open forests with greater spatial heterogeneity than the other species.

Gray Jay favored forest habitats (thick canopy, $p < 0.001$, REGRN) that contained spruce, either white spruce or black spruce. Most of the forest study plots, deciduous, coniferous, and mixed, had territories or portions of territories on them; the amount and species composition of spruce varied widely among the plots, from a mean frequency of occurrence on subplots of 7 to 100 and from totally white spruce to totally black spruce. Gray Jay habitats had a mean importance value for spruce of 46%--40% for white spruce and 6% for black spruce. The spruce relative importance value and general size stature of the forest were less than for most other coniferous species--White-winged Crossbill, Townsend's Warbler, and Boreal Chickadee--and the tree heterogeneity was much higher (Table IX). Sixty-seven percent of observations were in the tree layer and 15% below 1.2 m (mean height, 4.9 ± 2.7 m); 33% were in white spruce, 16% in black spruce, and 24% in aspen.

Boreal Chickadee favored habitats with forest characteristics and showed a strong preference for white spruce (Table IX). These habitat values were exceeded only by those for the White-winged Crossbill and Townsend's Warbler. Unlike these latter species, however, this chickadee had territories in Mixed-Deciduous Coniferous Forests as well as in Coniferous Forests and in black spruce as well as white spruce stands. Observations showed 80% use of White Spruce, 9% of aspen, 5% of willow, and 4% of black spruce. Ninety percent of birds observed were in the tree layer and 9% in the medium and tall shrub layers (mean height, 8.3 ± 3.4 m). Moss, which is used as a nest material, appeared to be a selected ground cover variable ($p < 0.001$, REGRN and DFA) independent of its high correlation with spruce forests.

Brown Creeper territories were too few to allow adequate definition of this species' habitat. Statistically, canopy thickness at 7.8 m--i.e., forest--was the only habitat variable significant at the $p < 0.001$

TABLE IX

Mean values of variables which best distinguished the habitats of birds of Coniferous Forest, upper Tanana River Valley, Alaska, 1977. Values are from species-present subplots and are followed by standard deviations.

Species	No. of subplots	Edge (0-1)	Stem diameter (mm)	Distance between trees (m)	Stem height (m)	Canopy thickness (m)	Total canopy coverage (%)	Relative importance value (%) White spruce	Relative importance value (%) Black spruce	Tree heterogeneity index
White-winged Crossbill	25	0.12±0.02	150±60	3.4± 1.1	14.4±5.1	11.5±4.8	65±16	67.2		31.5
Townsend's Warbler	89	0.03±0.00	150±50	3.4± 0.9	13.1±4.4	10.6±4.1	69±15	60.0		27.4
Boreal Chickadee	65	0.06±0.01	140±50	3.4± 1.0	12.4±4.6	9.7±4.4	63±15	54.4		29.5
Brown Creeper	25	0.00	130±40	3.6± 1.3	12.3±4.0	7.8±3.8	66±19	54.0		35.9
Gray Jay	93	0.23±0.05	120±60	4.2± 6.1	10.3±4.7	7.6±4.2	61±23	40.6		142.9
Ruby-crowned Kinglet	27	0.26±0.07	110±60	7.1±13.9	9.5±5.1	7.4±4.4	48±32	51.11		194.3

level (REGRN). Only 2.5 territories were delineated; two were on Upland White Spruce #1 plot (CF1) and one was on Upland Birch-White Spruce plot (MF2). Fifty-three percent of birds observed were in white spruce and 40% in paper birch.

Ruby-crowned Kinglet showed a strong selection for spruce habitats, either black or white spruce; species-present subplots had a combined spruce relative importance value of 62%, second only to White-winged Crossbill (Fig. 16). In general, however, kinglets favored more open forests of lesser stature than any of the other coniferous forest birds, including Gray Jay (Table IX), and it favored forests with a high tree heterogeneity. Ruby-crowned Kinglet territories occurred on almost all of the Mixed Deciduous-Coniferous Forest and Scattered Woodland and Dwarf Forest plots and on all Coniferous Forest plots, except the two densest white spruce plots. Sixty-two percent of kinglets observed were in spruce (48% in white spruce) and 38% were in deciduous trees (33% in paper birch) (ANOVA showed a slight tendency toward avoidance of aspen; $p < 0.05$). Ninety percent of observed activity was in the tree layer.

Townsend's Warbler clearly selected white spruce; 30% of the variation in its abundance was explained by this single factor ($p < 0.001$, REGRN). Its presence was restricted to mature coniferous or mixed-coniferous forests with large white spruce trees (CF1, CF2, MF2); the habitat described by measured variables was second only to that of the White-winged Crossbill in the relative importance value and size of the white spruce (Table IX). While statistics did not indicate paper birch as a significant variable, this tree had a relative importance value of 17%

on the species-present subplots and was used by foraging and singing birds; 60% of birds observed were in white spruce, 31% in paper birch. Ninety-five percent of Townsend's Warblers were observed in the tree layer, 4% in tall shrubs (mean height, 10.1 ± 3.7 m).

White-winged Crossbill appeared to be only a visitor on the study plots, where it showed a clear preference for mature forests of white spruce. Species-present subplots had the highest mean values for white spruce relative importance, tree height, and canopy thickness of any coniferous forest bird species. Observations showed 73% of activity in white spruce, 18% in willow, and 9% in black spruce. Distribution of height observations was 82% in the tree layer and 18% in the tall shrub layer (mean height, 11.8 ± 5.8 m).

Open Forests and Scattered Woodlands

The similar mean habitat values of five bird species placed them in an artificial grouping whose mean values describe an open forest or scattered woodland situation (Table X and Fig. 17), although this described situation itself is not a discrete habitat. The actual habitats of some of these species ranged from shrub thickets to forests. The Common Redpoll and Orange-crowned Warbler, for instance, utilized both shrub thickets and forest habitats, and the resultant arithmetic means of species-present subplots are similar to those of Scattered Woodland habitats--which both of these species also use. The situation is similar also for the American Robin; while it obviously favored aspen forests on the study area, the wide range of habitats utilized resulted

TABLE X

Multiple regression equations relating habitat variables to breeding density of 26 bird species in the upper Tanana River Valley, Alaska. The order in which the variables were entered into the equation is left to right. Numerals preceding the habitat variables are standardized slope values. All variables in the equations were statistically significant ($p \leq 0.05$); greater significance ($p \leq 0.001$) is indicated by boldface type. Equations are based on 331 observations, with the number of species-present subplots indicated by n.

SPECIES	EQUATION	R^2	n
Shrub Thicket Birds			
Alder Flycatcher	= -0.123 + 0.033 brush density + 0.088 willow + 0.224 water + 0.111 Balsam Poplar - 0.029 stem distance + 0.087 Thinleaf Alder + 0.079 grass	0.262	27
Yellow Warbler	= 1.088 + 0.309 Balsam Poplar - 0.054 tree distance + 0.520 Thinleaf Alder - 0.122 tree layer foliage volume + 0.242 low shrub layer foliage volume - 0.027 slope - 0.148 Black Spruce + 0.123 willow	0.467	34
Rusty Blackbird	= 2.452 + 0.245 Thinleaf Alder - 0.139 canopy coverage - 0.028 tree distance - 0.172 forbs - 0.147 Black Spruce - 0.014 slope + 0.301 water - 0.094 grass - 0.092 tree layer stem density - 0.071 willow	0.398	30
Savannah Sparrow	= - 0.179 + 0.214 Balsam Poplar - 0.098 canopy coverage+0.082 small, multiple-stemmedness - 0.325 water + 0.130 low shrub layer foliage volume + 0.048 stem distance - 0.017 tree distance + 0.069 tree layer stem density	0.232	15
Tree Sparrow	= 0.174 + 0.007 tree distance + 0.089 Thinleaf Alder - 0.029 canopy coverage + 0.058 Balsam Poplar	0.288	21
White-crowned Sparrow	= 2.869 - 0.277 canopy coverage - 0.199 Black Spruce - 0.018 slope - 0.595 water + 0.265 medium shrub layer stem density - 0.035 stem height	0.505	52
Fox Sparrow	= 0.609 - 0.021 tree distance + 0.139 Thinleaf Alder + 0.124 low shrub layer foliage volume - 0.012 slope - 0.102 Black Spruce - 0.240 water + 0.028 brush density - 0.070 canopy coverage	0.301	22

TABLE X

Continued

SPECIES	EQUATION	R^2	n
Lincoln's Sparrow	= 0.224 + 0.032 tree distance + 0.181 Balsam Poplar + 0.298 medium shrub layer stem density + 0.098 grass + 0.023 brush density - 0.097 Black Spruce + 0.245 water - 0.062 canopy coverage - 0.026 stem distance	0.667	49
Deciduous Forest Birds			
Hammond's Flycatcher	= - 0.041 + 0.093 Balsam Poplar + 0.087 large, multiple-stemmedness + 0.027 Quaking Aspen	0.081	13
Black-capped Chickadee	= 0.062 - 0.036 White Spruce + 0.006 slope	0.047	17
Hermit Thrush	= - 0.007 + 0.012 slope + 0.081 Balsam Poplar - 0.031 White Spruce	0.061	35
Yellow-rumped Warbler	= -0.247 + 0.159 tree layer foliage volume + 0.149 litter - 0.120 White Spruce + 0.115 stem diameter	0.254	147
Mixed Deciduous-Coniferous Forest Birds			
Varied Thrush	= 0.464 + 0.058 Paper Birch + 0.098 Black Spruce - 0.139 forb - 0.056 dwarf shrub + 0.049 Mountain Alder	0.100	47
Swainson's Thrush	= 2.362 + 0.242 litter - 0.369 Thinleaf Alder - 0.178 dwarf shrub - 0.100 single-stemmedness	0.191	212
Dark-eyed Junco	= 1.615 + 0.580 large, multiple stemmedness + 0.245 Mountain Alder - 0.321 Thinleaf Alder	0.157	198
Coniferous Forest Birds			
Gray Jay	= -0.162 + 0.144 canopy thickness + 0.280 Black Spruce + 0.038 slope - 0.118 tree layer foliage volume - 0.259 large, multiple-stemmedness	0.195	93

TABLE X

Continued

SPECIES	EQUATION	R^2	n
Boreal Chickadee	= -1.343 - 0.263 tree layer foliage volume + 0.069 slope + 0.353 moss + 0.151 White Spruce + 0.132 stem height	0.406	65
Brown Creeper	= 0.003 + 0.063 canopy thickness - 0.015 slope + 0.072 Mountain Alder - 0.072 litter ± 0.051 tree layer foliage volume - 0.090 large, multiple-stemmedness	0.150	25
Ruby-crowned Kinglet	= 0.481 + 0.076 Black Spruce - 0.046 canopy coverage - 0.053 low shrub layer foliage volume + 0.022 White Spruce - 0.010 stem distance	0.142	27
Townsend's Warbler	= -1.415 + 0.191 White Spruce + 0.054 slope + 0.133 tall shrub layer stem density + 0.257 canopy thickness - 0.191 large, multiple-stemmedness - 0.102 stem height	0.493	89
White-winged Crossbill	= - 0.819 + 0.176 White Spruce + 0.068 stem height + 0.032 brush density	0.201	25
Open Forest and Scattered Woodland Birds			
Common Flicker	= 0.496 + 0.096 Balsam Poplar - 0.060 tree layer stem density - 0.007 tree distance	0.054	28
American Robin	= 1.067 + 0.415 Quaking Aspen - 0.026 slope - 0.110 grass - 0.171 forb	0.472	99
Bohemian Waxwing	= 0.218 + 0.153 Quaking Aspen - 0.010 slope	0.123	22
Orange-crowned Warbler	= 2.244 - 0.225 White Spruce - 0.294 Thinleaf Alder + 0.144 willow + 0.292 large, multiple-stemmedness - 0.175 Paper Birch - 0.141 Black Spruce - 0.205 forb - 0.106 moss	0.300	153
Common Redpoll	= 0.012 + 0.126 dwarf shrub	0.025	38

TABLE X

Mean values of variables which best distinguished the habitats of birds of open forests and scattered woodlands, upper Tanana River Valley, Alaska, 1977 (see text for explanation of grouping). Values are from species-present subplots and are followed by standard deviations.

Species	No. of subplots	Dwarf shrub (% ground cover)	Edge (0-1)	Distance between stems ≥ 25.4 mm (m)	Distance between trees (m)	Canopy thickness (m)	Total canopy coverage (%)	Brush density @ 1 mm (stems x 10^3/ha)	Stem heterogeneity index	Tree heterogeneity index
Common Redpoll	38	31±17	0.21±0.05	4.6±8.0	5.8±11.3	6.4±2.7	63±24	14.58±17.16	176.7	194.7
Common Flicker	28	35±18	0.50±0.17	3.3±1.1	5.6±5.2	5.9±3.1	54±30	12.39±18.09	33.0	92.6
Orange-crowned Warbler	153	31±17	0.34±0.10	3.1±1.6	4.9±7.0	5.8±2.3	65±24	14.50±18.73	51.8	141.3
American Robin	99	36±17	0.39±0.12	3.1±2.2	6.2±11.5	5.3±2.2	62±26	14.18±20.21	68.5	184.0
Bohemian Waxwing	22	42±14	0.32±0.09	4.7±4.8	9.0±13.6	5.0±1.8	55±30	6.80±5.32	103.5	150.8

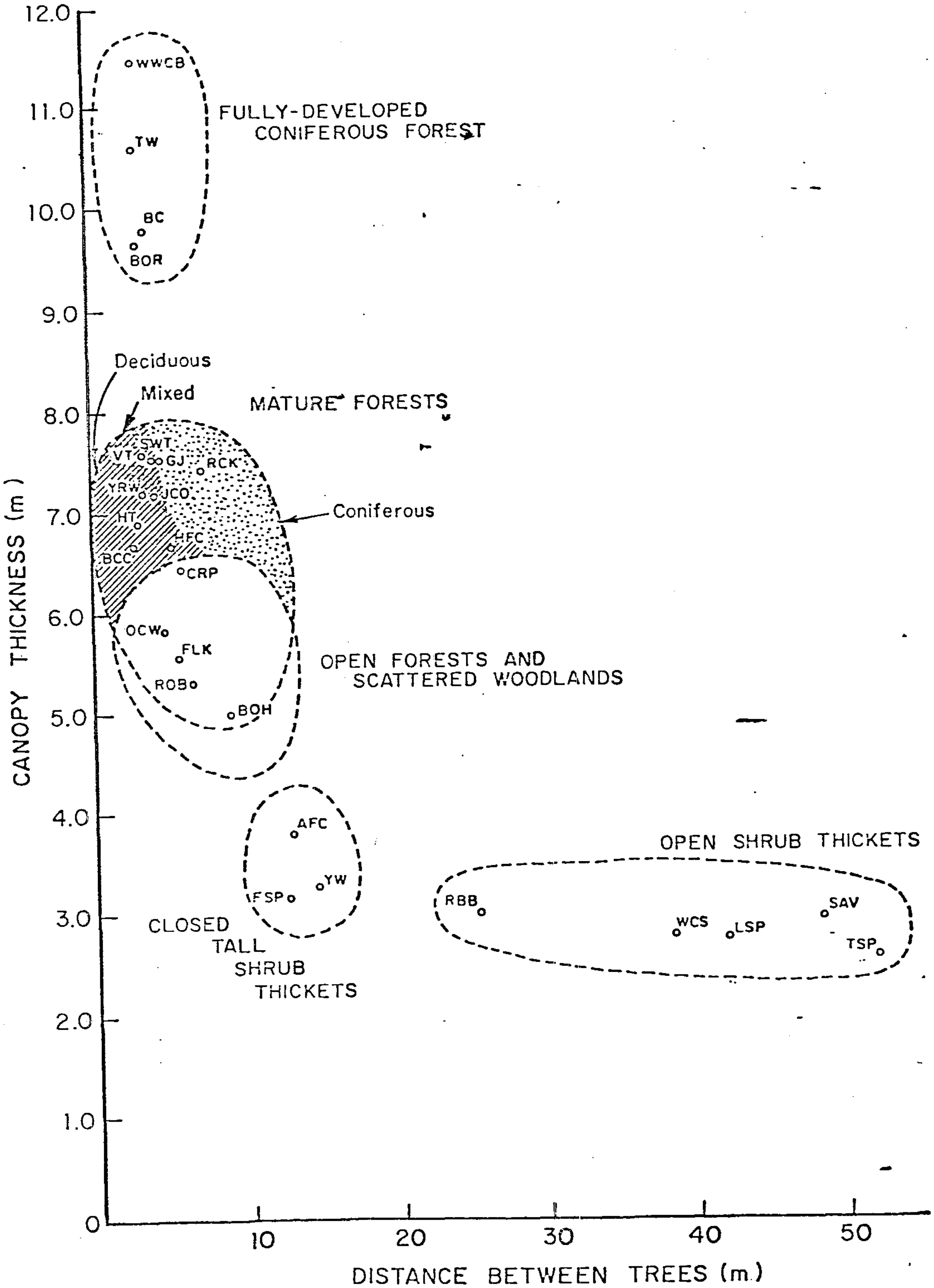

Figure 1. Habitat ordination of birds in the upper Tanana River Valley, Alaska, based on a bivariate plot of mean habitat variables "canopy thickness" and "distance between trees." Abbreviations for species are given in Table II.

in mean values for open forest or woodland situations--in which it was also found. The habitats of the Common Flicker and Bohemian Waxwing were more accurately described by the habitat means.

Common Flicker habitat was inadequately measured in this study; only 5% of its variability in abundance was explained by the measured habitat variables. Flicker occurrence, however, corresponded with the presence of large-diameter balsam poplar trees ($p < 0.009$, REGRN) in edge situations ($p < 0.005$, ANOVA) and with a ground cover of dwarf shrubs ($p < 0.01$, ANOVA and DFA) (Table X); these dwarf shrubs produced berries that were eaten by the flicker. Fifty percent of the birds observed were in the tree stratum and 20% were in tall shrubs; 32% were in poplar, 24% in aspen, and 19% on the ground.

American Robin showed a clear preference for quaking aspen ($p < 0.001$, REGRN and DFA), with this tree species accounting for 42% of the variability in robin abundance; it occurred in greatest densities on aspen plots DF2 and DF3 (6.5 and 4.9 territories/ 10 ha, respectively). There also appeared to have been a concomitant tendency to avoid closed spruce and birch forests ($p < 0.005$, ANOVA), probably because of the denser understory and lack of berry-producing dwarf shrubs; breeding densities were low in such habitats (DF4 and DF5, MF2 and MF4, and all CF plots). The robin is catholic in its choice of habitats in Alaska, and it was second only to the junco in the number of study plots on which it occurred (18 plots of 23, excluding MF5). Also, the spatial heterogeneity of trees in its habitat was exceeded only by Common Redpoll and Ruby-crowned Kinglet (Table X). Observations showed

54% of activity in the tree stratum and 44% below 2.5 m; 42% of birds seen were in aspen, 31% were on the ground, and 12% were in white spruce.

Bohemian Waxwing was only a visitor to most of the plots on the study area, and habitat measurements proved inadequate for statistical analyses. An examination of the mean habitat values of species-present subplots, however, gave some descriptive clues. Waxwings seemed to favor open tree habitats (distance between trees almost equal to tree height and large stem height and diameter) with fairly high spatial heterogeneity and a high dwarf shrub cover (highest for any bird species); many of the dwarf shrubs produced berries which were eaten by the waxwings. Sixty-three percent of birds were seen in aspen, 21% were on the ground, and 10% were on dead snags; 79% were in the tree stratum and 21% were below 1.2 m.

Orange-crowned Warbler favored habitats of willow shrub ($p < 0.001$, DFA). Territories occurred on almost all of the Shrub Thicket, Deciduous and Mixed Deciduous-Coniferous Forest, and Scattered Woodland and Dwarf Forest plots, but not on the Coniferous Forest plots. Statistical analyses, in fact, indicated an avoidance of spruce and of thinleaf alder (both $p < 0.001$, REGRN). Twenty-eight percent of birds observed were on aspen, 27% on birch, and 25% on willow; only 6% were on alder and 5% on spruce. Highest densities occurred on Tall Shrub Thicket plots (6.0-9.6 territories/10 ha). Height of activity was divided between the tree layer (72%) and the low-medium shrub layer (24%). Apparently Orange-crowned Warbler used willow shrubs wherever they occurred, whether in the open or under deciduous forest canopy, and the main breeding and maintenance activities were within the ground to medium shrub layer. Tree-height vegetation was not required, but was readily used when present for singing and foraging; on the other hand, birds were fairly common in some deciduous forests that lacked well-developed shrub understories (aspen plots DF1, DF2, and DF3).

Common Redpoll habitat analyses showed only one possibly discriminating variable (dwarf shrub), undoubtedly in part because of the small number of observations and the extreme lability of redpolls. In interior Alaska, for example, the redpoll may nest low at the base of a dwarf shrub or high in the axil of a branch of a tall tree; during summer in open shrub habitats it is a ground-brush forager, while in forests it is a foliage searcher (see Fig. 14). It occurred in most types of shrub thickets and forests, but it appeared to favor habitats with a higher than average dwarf shrub ground cover ($p < 0.004$, REGRN), although this variable accounted for less than 3% of the variability in redpoll abundance. Observations suggested a preference for deciduous woody plants: 40% of birds observed in trees or shrubs were in aspen, 29% in birch, 20% in willow, and 11% in white spruce, whereas the respective mean relative importance values of these plants on species-present subplots were 19%, 19%, 15%, and 30%. A similar preference pattern was noted in 1975 at Fairbanks (Spindler 1976).

Bird Species Habitat Ordinations

A principal component analysis reduced 21 structural habitat characteristics to three principal components accounting for 61.5% of total variation. Component I corresponded to a gradient of habitat openness, ranging from open treeless to closed forested habitats, and accounted for 36.6% of the total variance in habitat data. Component II corresponded with density of shrubs, accounting for an additional 14.6% of the variance. Component III reflected a gradient of canopy thickness and ground cover types and accounted for 10.3% of the variance in the data.

The habitat data for each bird species was projected onto ("scored against") the three principal components to ascertain where each species was located in the three-dimensional habitat space (Fig. 18). The groups of species characteristic of the six taiga habitats were separated distinctly.

A simple bivariate ordination of two mean habitat values, distance between trees and canopy thickness, produced a similar or superior separation of species groups and of species within groups than did the three-dimensional ordination by principal components (Fig. 17). The pattern of groups along the gradient and of species within each group is generally similar to the principal components ordination, with the exception of a more realistic representation of the Low and Medium Shrub Thickets species and the artificial open forest and scattered woodland species grouping. A similar ordination was obtained by plotting of medium and tall shrub stem density against canopy thickness.

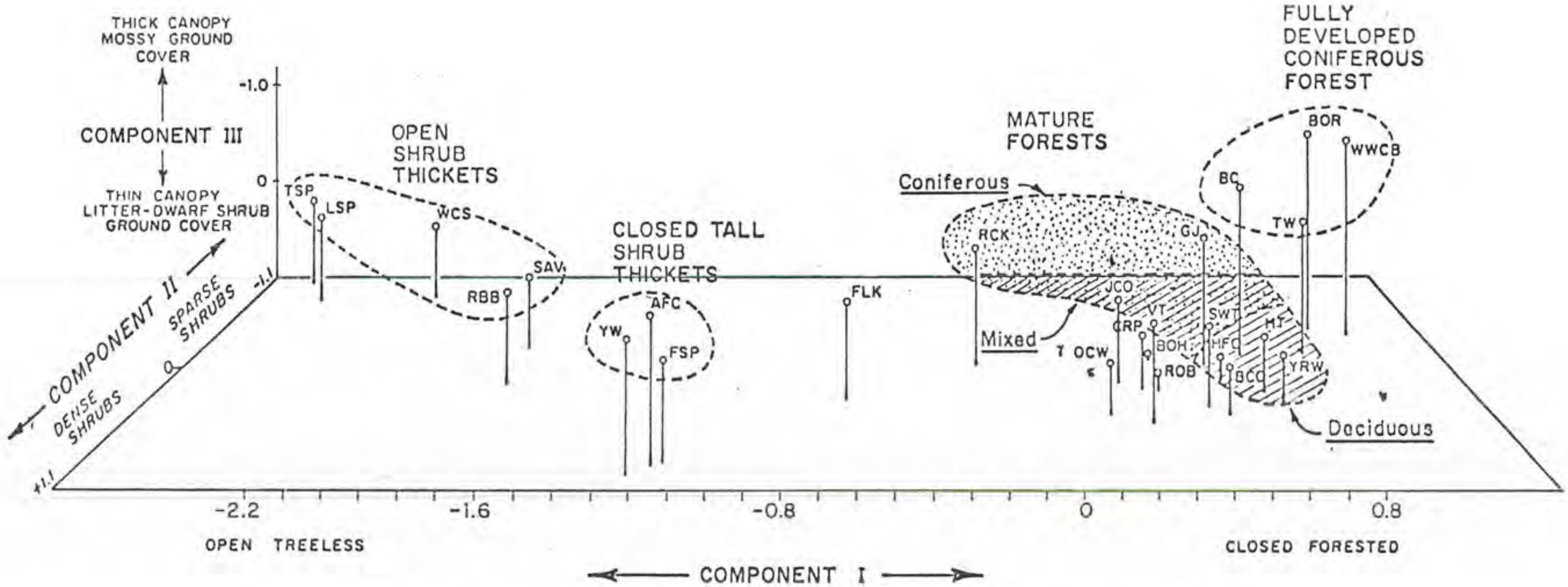

Figure 18. Habitat ordination of 26 taiga birds in the upper Tanana River Valley, Alaska, based on a three-dimensional plot of the centroids of factor scores along the first three principal component axes. Component I accounted for 36.6% of total variation; Component II, 14.6% of the variation; and Component III, 10.3% of the variation. Abbreviations for species are given in Table II.

DISCUSSION

A number of studies have shown that species richness and diversity in an avian community, as well as habitat selection by individual species, can be correlated with components of habitat structure, e.g., foliage-height diversity (MacArthur 1964, Karr 1968, Recher 1969, Willson 1974, Terborgh 1977), spatial heterogeneity (MacArthur 1964, Karr and Roth 1971, Roth 1976), height of vegetation (Lack 1933, Cody 1968 and 1979, Wiens 1969, James 1971, Flack 1976), percent cover of vegetation canopy (James 1971, Willson 1974), foliage volume (Sturman 1968, Balda 1969), and canopy thickness and tree density (Flack 1976). Community characteristics have also been shown to be affected by many other factors, such as stability and predictability of climate and other environmental factors, predation, competition, etc. (see discussions by Menge and Sutherland 1976, Wiens 1977, Pianka 1978) and by primary productivity and food resource levels (Terborgh 1977, Pianka 1978, and this study). Physical factors--e.g., soil temperature, moisture, pH, nutrient regime, slope, solar radiation--generally control rates of primary production in the vegetation of the Alaska taiga (Van Cleve, pers. comm.).

We used a number of the above-cited structural vegetation variables in our analyses, but also considered some physical aspects of the habitat (e.g., slope, aspect, water), importance values of tree and tall shrub species, and primary productivity. We found that breeding season avian occupancy of a habitat was apparently related mainly to the primary productivity of that habitat, an indirect relationship associated in some way with the amount of energy "available" in the habitat. Generally, species richness was increased with the structural complexity of the habitat, which allowed both the addition and expansion of foraging guilds, but richness was also increased in habitats of high primary productivity through guild expansion. Differences in species composition and habitat occupancy within a major habitat was also related to differences in primary productivity and differences in the structural diversity of the canopy (aspen vs birch stands), understory characteristics (berry-producing plants, dwarf shrub cover, etc.), and perhaps plant species composition (e.g., willow vs. other shrubs). Also, occupancy level and species richness differed between upland and lowland habitats of similar structure, primarily because of the prevalence of water in the lowlands and its absence on hillsides.

While taiga habitats of our study proved depauperate in terms of total breeding density and species richness compared to the temperate forests or more southern portions of the boreal forests of North America, tall shrub habitats were comparatively rich, equalling or exceeding southern counterparts in both breeding density and species richness. Tall Shrub Thickets supported the highest species richness and occupancy levels of any habitat in the upper Tanana River Valley. The high species richness and habitat occupancy undoubtedly resulted from a combination of high primary productivity, vertical structural diversity, spatial heterogeneity, and the influence of wetlands. Occupancy levels were particularly high in the lowlands and was significantly correlated with the presence of water, thinleaf alder, and balsam poplar. High primary productivity of these lowland sites was probably maintained in part by continual nutrient exchange in the alluvial wetland system; and the presence of nitrogen-fixing and highly-productive thinleaf alder may act as a catalyzing agent for other primary producers in the habitat--notably willow and poplar (Van Cleve, pers. comm.). Guild expansion appeared to be responsible for the high species richness observed, with 13 ground-bush foragers and three foliage searchers able to exploit the high energy resources of this vertically-limited but structurally diverse habitat.

Low and Medium Shrub Thickets had low species richness, apparently because of a relatively simple habitat structure. Unless standing water was present, this habitat was also relatively low in occupancy levels, probably because of the cold, boggy substrate. When water was present, as it frequently is in this habitat, occupancy and species richness were enhanced by the addition of the aquatic foraging guild.

Deciduous Forests were intermediate among the habitats in species richness and occupancy, and there was evidence of niche isolation among the few species in each foraging guild. The slightly lower levels of primary productivity but greater structural complexity of birch stands, compared to aspen stands, probably accounted for the correspondingly lower occupancy but greater species richness of the birch stands. The characteristic mid-story of mountain alder and the thick canopy of birch increased opportunities for the foliage searcher guild. Conversely, the lack of mid-story vegetation and the comparatively thin upper canopy of aspen stands resulted in a lower dominance of foliage searchers. The open understory and relatively high light levels in aspen stands, however, resulted in extensive growth of berry-producing dwarf and low shrubs, which were utilized by ground-brush foragers throughout the breeding season. Ground-brush foragers accounted for 79% of the estimated existence energy in aspen stands, a dominance exceeded only in the White Spruce-Birch Woodland.

Three of the four species that showed a primary preference for the Deciduous Forest habitat--Hammond's Flycatcher, Hermit Thrush, and Yellow-rumped Warbler--are more commonly inhabitants of mixed coniferous forests, or even coniferous forests, farther east (see, for example, Godfrey 1966, Erskine 1977,). These differences in habitat use are probably due to the lack of competition among inhabitants of the Deciduous Forest in eastern Alaska. The Hammond's Flycatcher, for instance, is occupying the niche used by the Dusky Flycatcher (Empidonax oberholseri) farther south (Johnson 1963, Godfrey 1966). Farther east, the Swainson's Thrush is more a bird of coniferous forests, while the Hermit Thrush is more in mixed forests (Dilger 1956). In interior Alaska, however, the Swainson's Thrush, while widespread, achieves its greatest abundance in the mixed forests, whereas the Hermit Thrush is in deciduous forests, perhaps to avoid competition with its congener. The Yellow-rumped Warbler appears to be exploiting the more productive deciduous forests of interior Alaska in the absence of most other forest warblers--except the recently established coniferous forest Townsend's Warbler.

The Mixed Deciduous-Coniferous Forest habitat was also intermediate in occupancy levels, but the diverse habitat structure of both deciduous and coniferous life forms supported a diverse avian community. High species richness was gained through both the addition and expansion of foraging guilds and was exceeded only by the Tall Shrub Thickets, which had much higher levels of primary productivity.

Scattered Woodland and Dwarf Forest was the third habitat with an intermediate level of avian occupancy, in spite of the fact that the open canopy of this habitat, with its concomitant greater presence of shrub layers, added characteristics of the more productive shrub thicket communities. The stunted character of the tree species in this habitat indicates low primary productivity, which may account, indirectly, for the relatively low species richness and the low number and size of the foraging guilds.

The low occupancy level in the Coniferous Forest habitat, and especially in the black spruce stands, appears indirectly related to low primary productivity rates. A thick canopy with a varied, conical structure and an open upper layer, however, provided foraging opportunities for five guilds.

The pattern of permanent resident species abundance during the breeding season appeared generally to correspond to their winter season patterns. Wintering birds near Fairbanks tend to be most numerous in white spruce forests, followed by black spruce and mixed white spruce-birch forests (pers. obs.). Gray Jay, Boreal Chickadee, and Northern Three-toed Woodpecker generally bred on the study area in the same white spruce-dominated forests in which they wintered, and the Coniferous Forests and Mixed Deciduous-Coniferous Forests, which support Pine

Grosbeak, redpoll, and White-winged Crossbill in winter, also support them in summer. The ability of a habitat to support resident wintering species is apparently largely related to the availability of a relatively high abundance of tree seeds, especially white spruce and paper birch, and probably also to the presence of the thick coniferous canopies, which minimize the loss of bird body heat by direct radiation to open sky, especially during roosting. Van Cleve and associates (pers. comm.) have found that spruce forests, especially white spruce, produce the highest above-ground biomass of forest plant growth, which would provide maximal foraging surface area for wintering birds. Also, seeds remain readily available in spruce cones and birch catkins throughout the winter. White spruce seeds provide more calories (av. 6615 cal/gm dry wt) than black spruce seeds (av. 6053 cal/gm dry wt) (Brink and Dean 1966); paper birch seeds provide 5637 cal/gm dry wt (av. five samples, range 5586-5710 cal/gm dry wt, Kessel unpubl. data). Brink and Dean (op. cit.) found that Red Squirrels (Tamiasciurus hudsonicus) could maintain or increase body weight when fed a pure diet of white spruce seeds, but lost weight on black spruce seeds.

Annual variation in breeding densities of individual species may alter the species composition and perhaps the community structure of a habitat from year to year, but since the most abundant species are the least variable, the impact of this variation should be minimal. The inverse relationship between abundance and annual variation may be caused by density-dependent regulation limiting and stabilizing breeding population levels for abundant species (Stephen F. MacLean, pers. comm.).

In contrast, uncommon species are more likely to be influenced by varying environmental conditions.

Both a bivariate and the multivariate bird species breeding habitat ordinations successfully separated the species groups characteristic of the major taiga habitats. The Tall Shrub Thicket, Deciduous Forest, and Mixed Deciduous-Coniferous Forest species ordinated into separate tight clusters, indicating the consistency of and their fidelity to the habitat that they occupied. The Coniferous Forest and Low and Medium Shrub Thicket birds were dispersed over a larger portion of the gradient, possibly indicating the wider variety of statures for these habitats. The final group of species inhabited a wide range of habitats, the mean of which is in an artificial habitat resembling open forests and scattered woodlands. Some species in this group may be considered habitat-generalists (e.g., American Robin, Orange-crowned Warbler, and Common Redpoll), for they occurred in habitats ranging from Tall Shrub Thicket, through Scattered Woodland and Dwarf Forest, to mature forests. James (1971), Whitmore (1977), and Anderson and Shugart (1974), from studies in essentially single habitats, did not detect discrete species groupings in their principal components ordinations. The discrete grouping for the taiga data indicates that we were not describing a continuum of one major habitat and its successional stages in the sense of Bond (1957), but a group of distinct habitat structures arrayed along a gradient of increasing habitat complexity. Furthermore, these habitats and their corresponding bird utilization are different enough (and each perhaps simple enough) that a bivariate ordination sufficed to produce a similar or superior separation of species groups and of species within groups.

Boreal bird species have been categorized as habitat-generalists (Theberge 1976, Erskine 1977), being nearly ubiquitous in terms of habitat preferences. The relatively small number of species breeding in the taiga may allow widely-separated niches and a tendency towards lack of habitat specificity, but our habitat use and community structure data suggest that in the Alaska taiga most breeding species have distinct habitat preferences. Even habitat-generalists reach maximum abundance in habitats of specific structure and composition.

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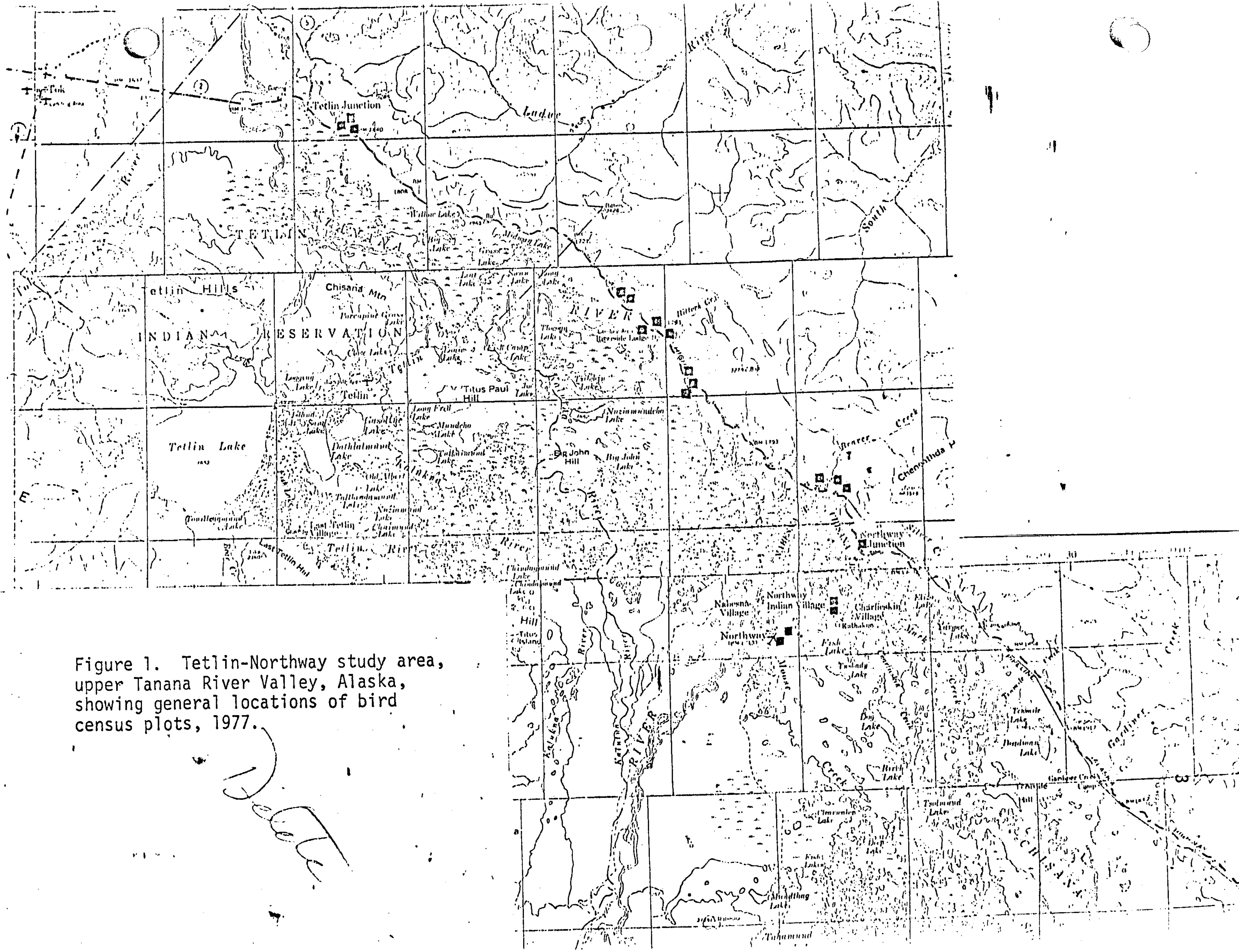


Figure 1. Tetlin-Northway study area, upper Tanana River Valley, Alaska, showing general locations of bird census plots, 1977.

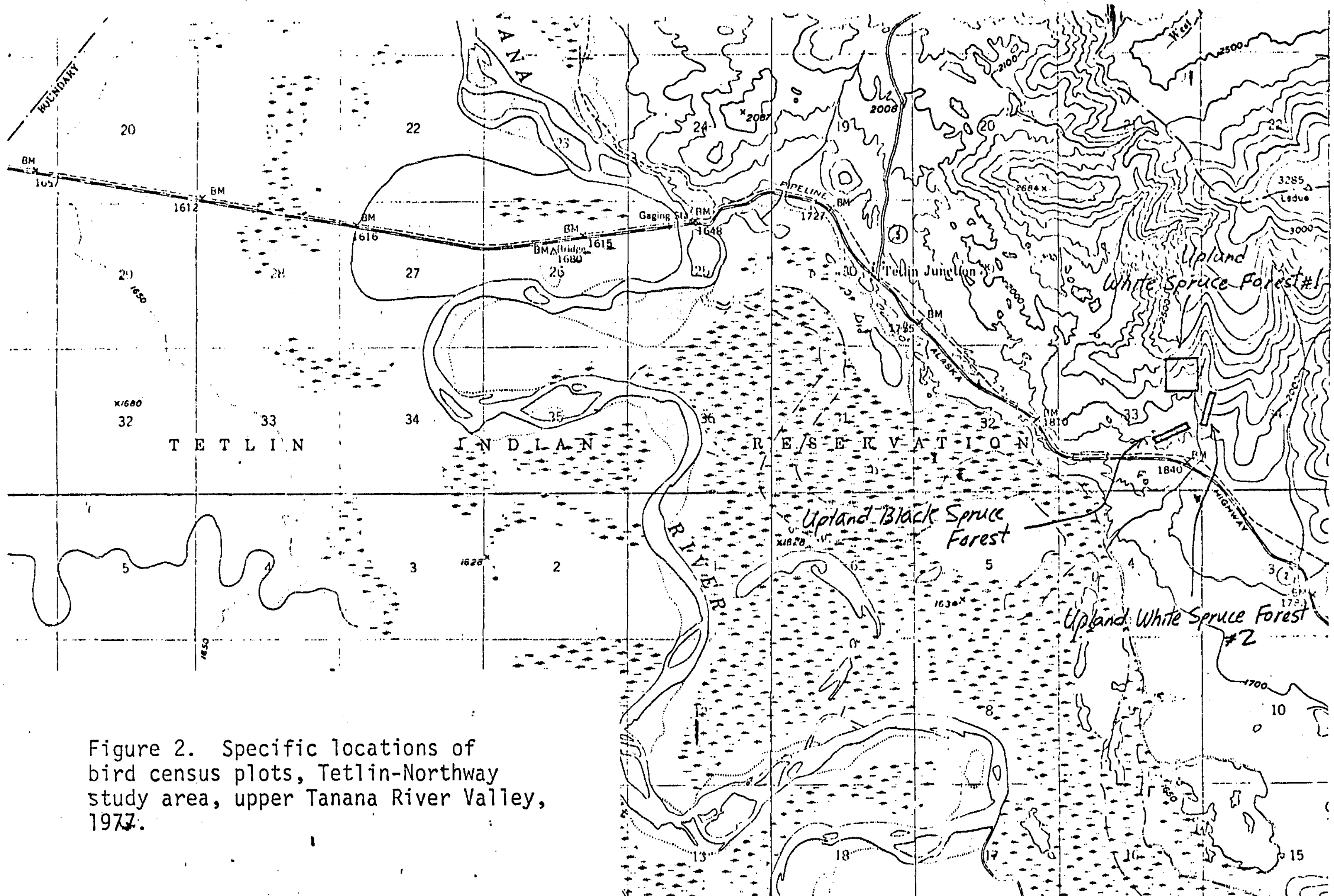
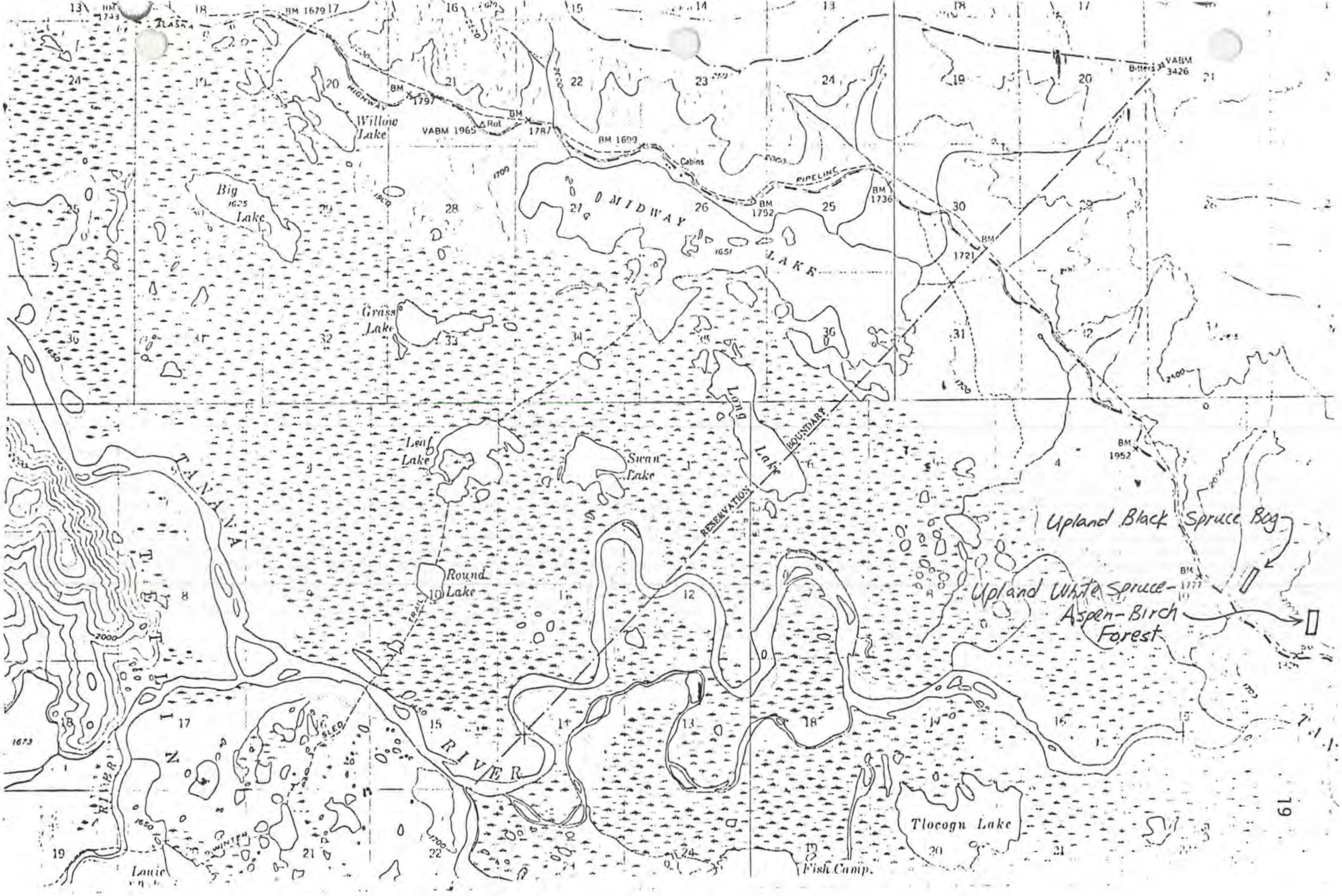


Figure 2. Specific locations of bird census plots, Tetlin-Northway study area, upper Tanana River Valley, 1977.



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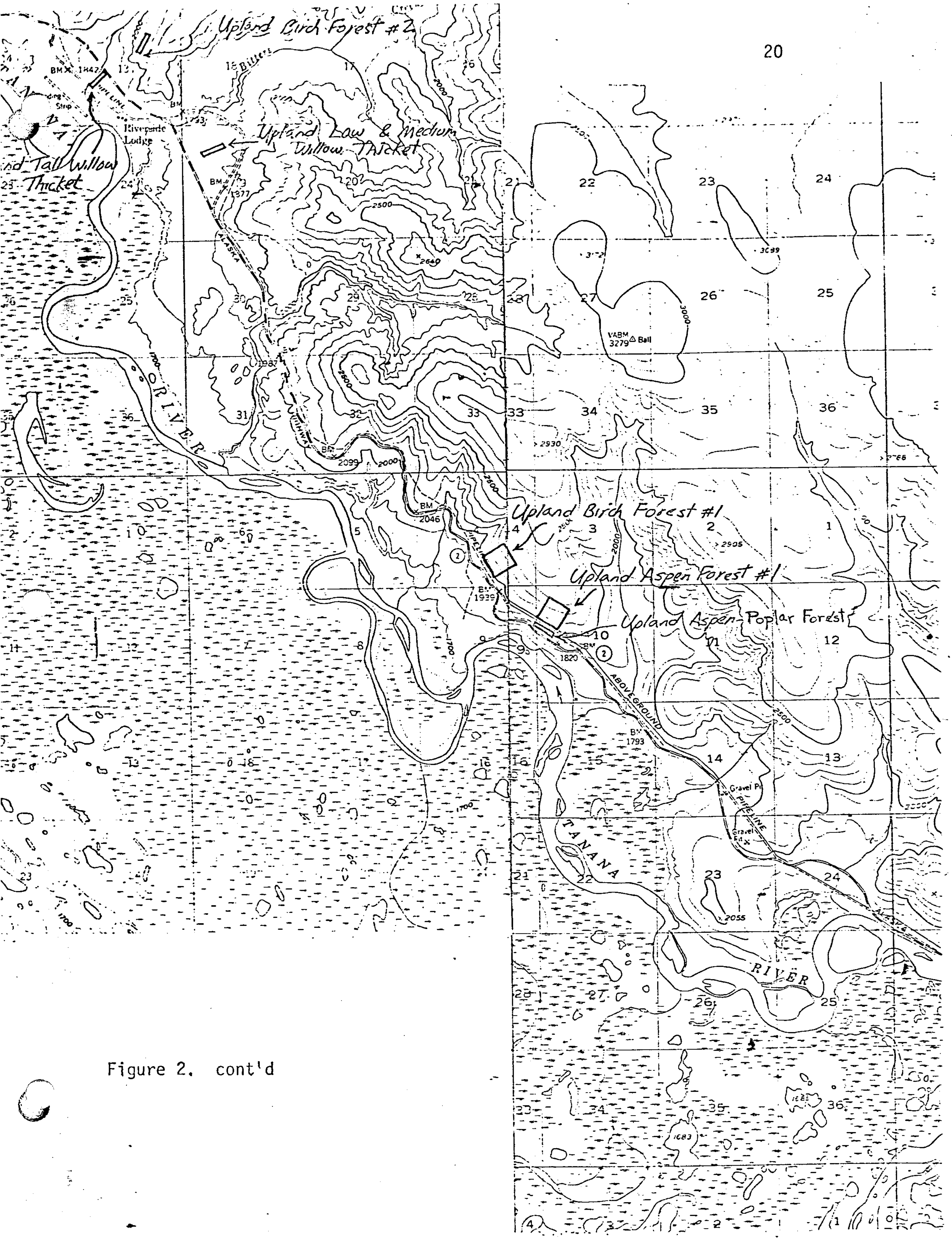

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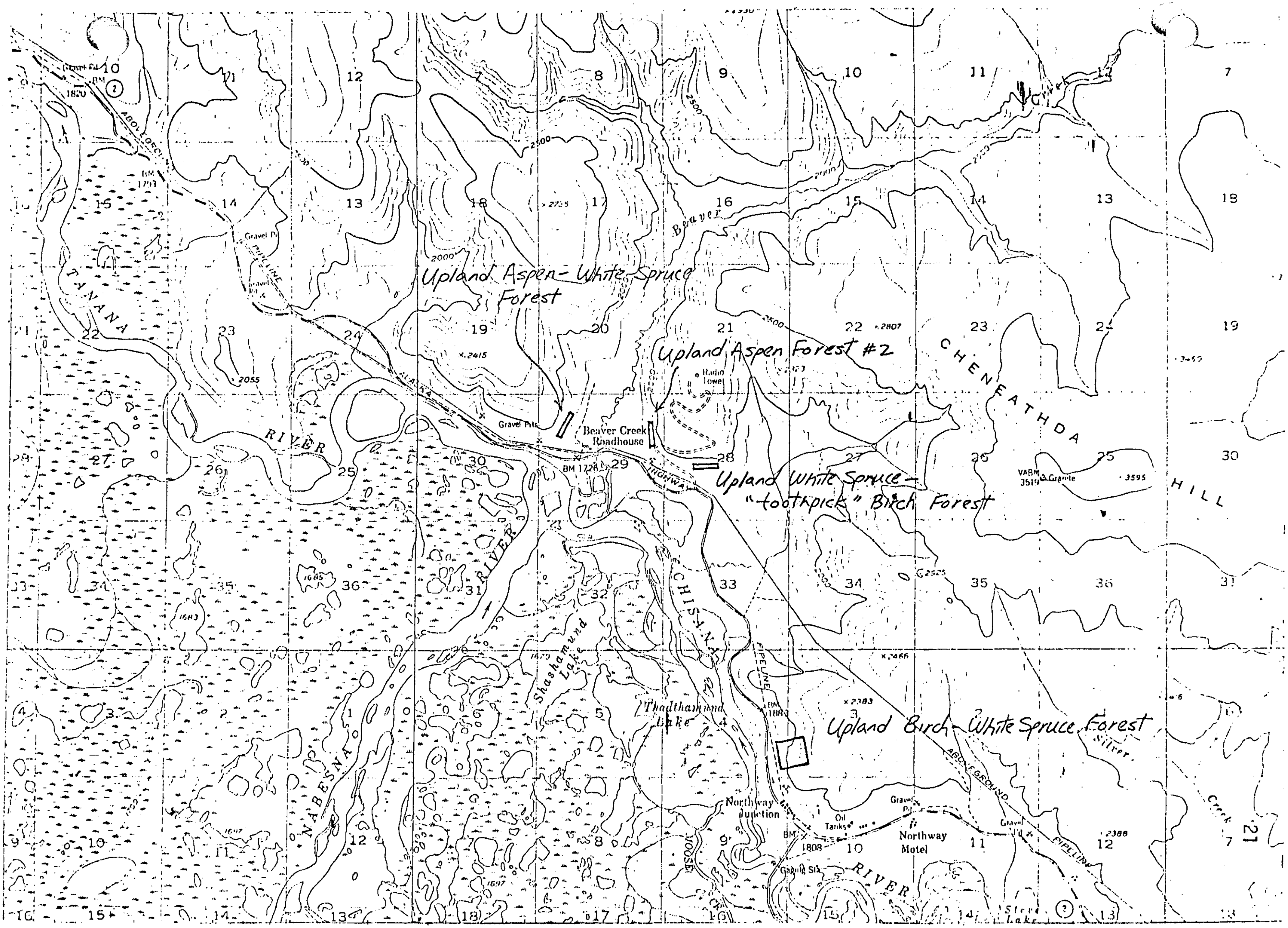

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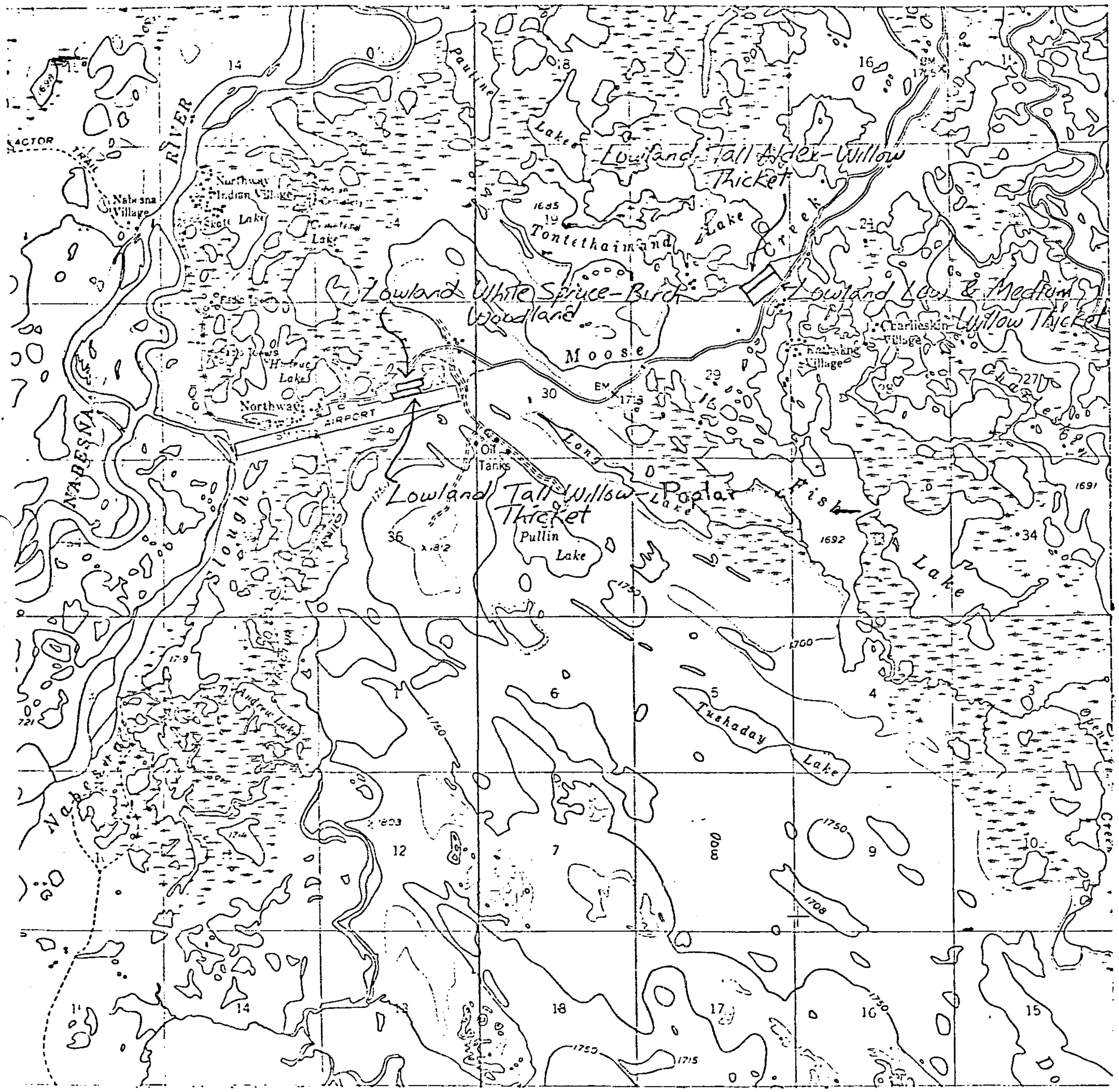

Figure 2. cont'd

Table 1. Summary of values of habitat variables from each bird census plot, Tetlin-Northway study area, Alaska, August 1977

Variable	Symbol	SHRUB THICKETS: Lowland Medium-Tall Willow	SHRUB THICKETS: Lowland Tall Willow-Poplar	SHRUB THICKETS: Upland Tall Willow	SHRUB THICKETS: Upland Low & Medium Willow
Ground Cover (in percent)					
Grass*	GRASS	19.1	13.2	35.1	53.2
Herbs*	HERBS	13.6	14.4	12.5	7.6
Moss and Lichen*	MOSS&L	15.8	12.1	22.5	7.6
Dwarf Shrub (<0.5 high)*	DSHRUB	25.9	35.0	22.5	31.6
Litter*	LITTER	19.3	25.3	6.2	0.0
Water, standing*	WATER	6.3	0.0	1.2	0.0
Fire Evidence (0=minimum, 2.0=maximum)	FIRE	0.03	0.0	0.0	0.0
Edge (0=minimum, 2.0=maximum)	EDGE	0.35	1.0	0.71	1.0
Woody Growth Form (percent of stems)					
Single Stem, large or small diameter	SS	47.2	48.2	26.8	60.7
Multiple Stem, small diameter	MSS	52.8	51.8	73.2	39.3
Multiple Stem, large diameter	MSL	0.0	0.0	0.0	0.0
Slope, average (%)*	SLOPE	0	0	0	0
Aspect, average azimuth (0-360°)*	ASPECT	flat	flat	flat	flat
Tree/Shrub Diameter (cm dbh)*	DIAMETER	4	5	4	4
Distance between Trees/Shrubs (≥2.54 cm dbh definition) (m)*	DISTANCE	15.1	3.9	3.1	14.1
Distance between Trees (>4.6 m height) (m)	TRDISTANCE	42.8	5.0	6.0	49.3
Tree/Shrub Height (m)	HEIGHT	3.7	4.7	4.4	3.3
Distribution of Tree/Shrub Height (% in each class)					
>30 m	H>30	0.0	0.0	0.0	0.0
20.1-30 m	H20-30	0.0	0.0	0.0	0.0
10.1-20 m	H10-20	0.3	0.0	1.8	0.0
4.7-10 m	HT	17.5	60.7	33.9	14.3
2.5-4.6 m	HTS	68.1	39.3	57.1	46.4
0-2.4 m	HLMS	13.4	~~0.0~~	7.1	39.3
Height Diversity (H')	HDIV	0.853	0.670	0.947	1.001
Canopy Thickness (m)	THICK	2.7	3.7	3.3	2.9
~~Total~~ Canopy Coverage (~~% of sky observed~~)**	CANOPY	22.5	25.7	42.9	4.3
Distribution of Foliage Volume (% in each class)					
>4.6 m†	FV4	4.0	0.0	4.7	0.0
2.5-4.6 m†	FV3	19.4	17.6	39.1	3.7
1.1-2.4 m†	FV2	21.6	25.5	28.1	14.8
0-1.0 m†	FV1	54.9	56.9	28.1	81.5
Foliage Diversity (H')†	FDIV	1.107	0.975	1.224	0.571
Brush Density, 0-1.0 m ~~high~~ (stems/ha)	BRUSH	~~24012.~~	~~30335.~~	~~33158.~~	~~9523.~~
Tree/Shrub Density, >2.54 cm dbh (stems/ha)	TRDENS	44	672	1012	50
Distribution of Tree/Shrub Density (% in each class)					
>4.6 m (tree layer)	DT	14.4	43.6	32.1	10.7
2.5-4.6 m (tall shrub layer)	DTS	72.2	56.4	60.8	50.0
1.1-2.4 m (medium shrub layer)	DLMS	13.4	0.0	7.1	39.3
Density Diversity (H')	DDIV	0.787	0.685	0.855	0.953
Basal Area of Trees/Shrubs (cm²/ha)*	BASAL	740	14794	29528	811
Tree and Tall Shrub Species Relative Importance (%)					
White Spruce*	WSPRUCE	16.7	2.6	30.4	66.1
Black Spruce*	BSPRUCE	0.0	0.0	0.0	0.0
Paper Birch*	BIRCH	1.8	16.5	0.0	0.0
Quaking Aspen*	ASPEN	0.0	0.0	0.0	0.0
Willow*	WILLOW	18.9	47.1	69.6	33.9
Balsam Poplar*	POPLAR	26.0	33.8	0.0	0.0
*Alnus incana**	INCANA	36.6	0.0	0.0	0.0
*Alnus crispa**	CRISPA	0.0	0.0	0.0	0.0
Tree/Tall Shrub Diversity (H')†	TSDIV	1.404	1.113	0.614	0.640
Stand Age (years)		(low/med shrub) (tall shrub)			
Mean Age	MAGE	148 82	27	42	44
Maximum Age	XAGE	200 180	36	65	60
Index of Heterogeneity (stems/DIST)††	SHET	97.9	27.7	53.3	74.7
Index of Heterogeneity (trees/TRDIST)††	THET	76.7	36.5	56.1	6.2

*See Ohmann and Ream (1971)
†See MacArthur (1964)
**See James and Shugart (1970)
††See Roth (1976)

Table 1. (cont'd)

Variable	Symbol	DECIDUOUS FOREST Upland Aspen-Poplar	Upland Aspen #1	Upland Aspen #2	Upland Birch #1	Upland Birch #2
Ground Cover (in percent)						
Grass	GRASS	17.5	6.1	5.3	10.7	7.6
~~Herbs~~ Forbs	~~HERBS~~	5.0	12.0	14.7	12.0	17.7
Moss and Lichens	MOSS&L	3.8	2.0	6.6	8.1	12.7
Dwarf Shrub (<0.5 m high)	DSHRUB	37.5	47.2	29.3	22.6	17.7
Litter	LITTER	26.2	32.7	44.1	46.6	44.3
Water, standing	WATER	0.0	0.0	0.0	0.0	0.0
Fire Evidence (0=minimum, 2.0=maximum)	FIRE	2.0	1.14	2.0	1.76	0.5
Edge (0=minimum, 2.0=maximum)	EDGE	1.0	0.33	0.71	0.14	0.0
Woody Growth Form (percent of stems)						
Single Stem, large or small diameter	SS	75.0	91.3	96.4	37.0	60.7
Multiple Stem, small diameter	MSS	8.9	5.9	0.0	40.5	28.6
Multiple Stem, large diameter	MSL	16.1	2.8	3.6	22.5	10.7
Slope, average (%)*	SLOPE	25	23	24	23	24
Aspect, average azimuth (0-360°)*	ASPECT	215	199	264	242	283
~~Tree/Shrub Diameter~~ (cm dbh)*	DIAMETER	13	12	9	12	11
Distance between ~~Trees/Shrubs~~ (>2.54 cm dbh ~~definition~~) (m)*#	DISTANCE	2.9	2.8	1.7	2.9	2.4
Distance between Trees (>4.6 m height) (m)	TRDISTANCE	2.9	2.9	1.7	3.2	2.6
~~Tree/Shrub Height (m)~~	HEIGHT	12.0	11.7	10.4	10.4	10.1
Distribution of ~~Tree/Shrub Height~~ (% in each class)						
>30 m	H>30	0.0	0.0	0.0	0.0	0.0
20.1-30 m	H20-30	3.6	0.0	0.0	3.3	0.0
10.1-20 m	H10-20	58.9	60.7	53.6	38.3	48.2
5.0 ~~4.7~~-10 m	HT	26.8	34.4	39.3	42.9	42.9
2.5-4.9 m	HTS	10.7	4.3	7.1	14.3	7.1
0-2.4 m	HLMS	0.0	0.6	0.0	1.3	1.8
Height Diversity (H')	HDIV	1.023	0.836	0.889	1.178	0.975
Canopy Thickness (m)	THICK	6.4	5.4	4.6	7.7	6.3
Total Canopy Coverage (% of sky observed)**	CANOPY	74.3	71.2	75.7	78.6	81.4
Distribution of Foliage Volume (% in each class)†						
≥5.0 ~~4.9~~ m†	FV4	65.2	65.2	66.2	56.2	60.6
2.5-4.9 m†	FV3	9.1	9.7	9.1	21.2	17.0
1.0-2.4 m†	FV2	7.6	8.6	7.8	8.6	8.5
0-1.0 m†	FV1	18.2	16.5	16.9	14.0	13.8
Foliage Diversity (H')†	FDIV	1.003	1.013	0.991	1.139	1.088
Brush Density, 0-1.0 m high (stems/ha)	BRUSH	7732 ~~5937~~	7340 ~~5594~~	9549 ~~7407~~	9680 ~~7539~~	7732 ~~5937~~
~~Tree/Shrub Density~~, >2.54 cm dbh (stems/ha)‡#	TRDENS	1225	1243	3403	1158	1696
Distribution of ~~Tree/Shrub~~ Density (% in each class)						
≥5.0 ~~4.6~~ m (tree layer)	DT	83.9	94.1	87.5	81.1	89.3
2.5-4.9 m (tall shrub layer)	DTS	16.1	5.4	12.5	17.6	8.9
1.0-2.4 m (medium shrub layer)	DLMS	0.0	0.5	0.0	1.3	1.8
Density Diversity (H')	DDIV	0.441	0.241	0.377	0.532	0.389
Basal Area of ~~Trees/Shrubs~~ (cm^2/ha)*#	BASAL	206382	168679	279860	183793	187515
Tree and Tall Shrub Species Relative Importance (%)##						
White Spruce*	WSPRUCE	0.0	14.3	7.0	2.5	3.9
Black Spruce*	BSPRUCE	0.0	0.0	0.0	0.0	0.0
Paper Birch*	BIRCH	0.0	1.1	0.0	53.8	55.9
Quaking Aspen*	ASPEN	58.5	72.7	76.6	1.1	0.0
Willow*	WILLOW	16.3	9.1	6.3	16.9	24.9
Balsam Poplar*	POPLAR	25.2	1.9	10.1	0.7	0.0
*Alnus incana**	INCANA	0.0	0.0	0.0	0.0	0.0
*Alnus crispa**	CRISPA	0.0	0.9	0.0	24.9	15.3
Tree/Tall Shrub Diversity (H')†	TSDIV	0.957	0.895	0.796	1.157	1.035
Stand Age (years)						
Mean Age	MAGE	100	96	59	84	58
Maximum Age	XAGE	105	107	72	125	76
Index of Heterogeneity (stems/DIST)‡‡	SHET	13.2	22.0	44.1	32.1	32.4
Index of Heterogeneity (Trees/TRDIST)‡‡	THET	13.2	20.8	44.1	28.4	20.8

Table 1. (cont'd)

Variable	Symbol	MIXED DECIDUOUS-CONIFEROUS FOREST: Upland Aspen-White Spruce	Upland Birch-White Spruce	Upland White Spruce-Aspen-Birch	Upland White Spruce-"Toothpick" Birch
Ground Cover (in percent)					
Grass*	GRASS	14.6	10.2	2.7	1.2
Herbs*	HERBS	10.1	13.2	10.7	8.9
Moss and Lichens*	MOSS&L	14.6	19.2	17.9	11.4
Dwarf Shrub (<0.5 high)*	DSHRUB	19.1	15.0	38.3	27.8
Litter*	LITTER	41.6	42.4	30.4	50.7
Water, standing*	WATER	0.0	0.0	0.0	0.0
~~Fire Evidence (0=minimum, 2.0=maximum)~~	FIRE	2.0	0.0	2.0	2.0
~~Edge (0=minimum, 2.0=maximum)~~	EDGE	0.25	0.04	0.2	0.1
Woody Growth Form (percent of stems)					
Single Stem, large or small diameter	SS	84.4	62.3	47.5	78.5
Multiple Stem, small diameter	MSS	7.8	28.5	50.0	3.6
Multiple Stem, large diameter	MSL	7.8	9.2	2.5	17.9
~~Slope, average (%)~~*	SLOPE	32	17	23	19
Aspect, ~~average~~ azimuth (0-360°)*	ASPECT	105	282	292	184
Tree/Shrub Diameter (cm dbh)*	DIAMETER	11[illegible]	11[illegible]	9[illegible]	9[illegible]
Distance between Trees/Shrubs (≥2.54 cm dbh definition) (m)*	DISTANCE	2.6	2.6	2.7	2.1
Distance between Trees (>4.6 m height) (m)	TRDISTANCE	3.0	3.0	3.3	2.1
Tree/Shrub Height (m)	HEIGHT	10.0	10.2	7.2	8.6
Distribution of Tree/Shrub Height (% in each class)					
>30 m	H>30	0.0	0.0	0.0	0.0
20.1-30 m	H20-30	4.7	6.6	0.0	0.0
10.1-20 m	H10-20	32.8	38.0	25.0	25.0
4.7-10 m	HT	43.8	33.9	41.3	64.3
2.5-4.6 m	HTS	18.8	20.4	32.5	8.9
0-2.4 m	HLMS	0.0	1.0	1.3	1.8
Height Diversity (H')	HDIV	1.185	1.284	1.134	0.918
Canopy Thickness (m)	THICK	6.6	7.7	5.5	5.9
Total Canopy Coverage (% of sky observed)**	CANOPY	68.8	78.8	57.0	78.6
Distribution of Foliage Volume (% in each class)					
>4.6 m†	FV4	53.9	54.2	30.4	52.6
2.5-4.6 m†	FV3	19.7	20.4	31.3	20.5
1.1-2.4 m†	FV2	10.5	11.6	24.1	11.5
0-1.0 m†	FV1	15.8	13.8	14.3	15.4
~~Foliage Diversity (H')~~†	FDIV	1.181	1.179	1.347	1.200
Brush Density, 0-1.0 m high (stems/ha)	BRUSH	~~11420~~ 14.722	~~7035~~ 9.031	~~14321~~ 18.462	~~9523~~ 12.277
~~Tree/Shrub Density, ≥2.54 cm dbh (stems/ha)~~*	TRDENS	1451	1443	1372	2178
Distribution of Tree/Shrub Density (% in each class)					
>4.6 m (tree layer)	DT	78.1	74.5	61.2	87.5
2.5-4.6 m (tall shrub layer)	DTS	21.9	24.5	37.5	12.5
1.1-2.4 m (medium shrub layer)	DLMS	0.0	1.0	1.3	0.0
~~Density Diversity (H')~~	DDIV	0.526	0.405	0.725	0.377
Basal Area of Trees/Shrubs (cm²/ha)*	BASAL	218077	227359	139768	184042
Tree and Tall Shrub Species Relative Importance (%)					
White Spruce*	WSPRUCE	29.8	30.1	36.1	43.5
Black Spruce*	BSPRUCE	0.0	0.0	0.0	0.0
Paper Birch*	BIRCH	2.7	44.6	8.6	37.5
Quaking Aspen*	ASPEN	41.1	0.0	9.5	3.8
Willow*	WILLOW	9.7	3.4	24.9	15.2
Balsam Poplar*	POPLAR	16.7	0.0	3.5	0.0
*Alnus incana**	INCANA	0.0	0.0	0.0	0.0
*Alnus crispa**	CRISPA	0.0	21.9	17.5	0.0
~~Tree/Tall Shrub Diversity (H')~~	TSDIV	1.349	1.169	1.571	1.141
Stand Age (years)			(Burn 1) Both (Burn 2)		
Mean Age	MAGE	63	106 91 57	54	50
Maximum Age	XAGE	80	130	57	75
Index of Heterogeneity ~~(stems/DIST)~~††	SHET	28.3	30.7	47.9	42.0
Index of Heterogeneity (trees/~~TRDIST~~)††	THET	39.8	32.3	14.6	42.0

Table 1. (cont'd)

Variable	Symbol	CONIFEROUS FOREST			SCATTERED WOODLAND AND DWARF FOREST	
		Upland White Spruce #1	Upland White Spruce #2	Upland Black Spruce	Upland Black Spruce Bog	Lowland Spruce-[illegible] Woodl[illegible]
Ground Cover (in percent)						
Grass*	GRASS	11.9	5.2	10.1	21.0	7.9
Herbs*	HERBS	11.3	10.4	12.7	13.9	6.5
Moss and Lichens*	MOSS&L	38.1	49.3	38.0	25.7	18.4
Dwarf Shrub (<0.5 high)*	DSHRUB	22.6	7.8	29.1	30.2	58.0
Litter*	LITTER	15.9	27.3	10.1	8.1	9.2
Water, standing*	WATER	0.2	0.0	0.0	1.1	0.0
Fire Evidence (0=minimum, 2.0=maximum)	FIRE	0.14	0.86	0.0	0.0	1.29
Edge (0=minimum, 2.0=maximum)	EDGE	0.0	0.29	0.3	0.1	1.0
Woody Growth Form (percent of stems)						
Single Stem, large or small diameter	SS	88.5	86.5	98.2	98.2	100.0
Multiple Stem, small diameter	MSS	9.5	7.0	1.8	1.8	0.0
Multiple Stem, large diameter	MSL	2.0	7.0	0.0	0.0	0.0
Slope, average (%)*	SLOPE	29	38	8	2	0
Aspect, average azimuth (0-360°)*	ASPECT	165	283	185	224	flat
Tree/Shrub Diameter (cm dbh)*	DIAMETER	16	16	8	5	5
Distance between Trees/Shrubs (≥2.54 cm dbh definition) (m)*	DISTANCE	3.3	2.7	1.9	1.7	4.9
Distance between Trees (>4.6 m height) (m)	TRDISTANCE	3.7	2.9	2.4	7.4	9.0
Tree/Shrub Height (m)	HEIGHT	14.6	15.0	6.7	3.6	3.7
Distribution of Tree/Shrub Height (% in each class)						
>30 m	H>30	3.8	0.0	0.0	0.0	0.0
20.1-30 m	H20-30	29.1	37.5	0.0	0.0	0.0
10.1-20 m	H10-20	24.2	26.8	12.5	0.0	0.0
4.7-10 m	HT	28.1	19.6	60.7	19.6	42.9
2.5-4.6 m	HTS	14.5	12.5	23.2	67.9	35.7
0-2.4 m	HLMS	0.3	3.6	3.6	12.5	21.4
Height Diversity (H')	HDIV	1.481	1.420	1.022	0.842	1.061
Canopy Thickness (m)	THICK	12.3	11.7	4.9	2.6	2.9
Total Canopy Coverage (% of sky observed)**	CANOPY	61.2	74.3	40.0	15.7	1.4
Distribution of Foliage Volume (% in each class)						
>4.6 m†	FV4	51.0	57.5	28.6	2.9	0.0
2.5-4.6 m†	FV3	16.9	16.3	22.2	11.8	5.9
1.1-2.4 m†	FV2	13.3	16.3	22.2	35.3	11.8
0-1.0 m†	FV1	18.8	10.0	27.0	50.0	82.4
Foliage Diversity (H')†	FDIV	1.226	1.140	1.380	1.069	0.579
Brush Density, 0-1.0 m high (stems/ha)	BRUSH	~~6299~~ 8120	11992 (15450)	15874 (20464)	25044 (32286)	5291 (6824)
Tree/Shrub Density, ≥2.54 cm dbh (stems/ha)*	TRDENS	904	1357	2899	3403	424
Distribution of Tree/Shrub Density (% in each class)						
>4.6 m (tree layer)	DT	82.6	80.3	69.6	12.5	32.1
2.5-4.6 m (tall shrub layer)	DTS	17.1	16.1	26.8	75.0	42.9
1.1-2.4 m (medium shrub layer)	DLMS	0.3	3.6	3.6	12.5	25.0
Density Diversity (H')	DDIV	0.477	0.590	0.725	0.736	1.074
Basal Area of Trees/Shrubs (cm^2/ha)*	BASAL	287809	427725	186724	71198	18825
Tree and Tall Shrub Species Relative Importance (%)						
White Spruce*	WSPRUCE	74.0	66.6	9.5	0.0	73.4
Black Spruce*	BSPRUCE	0.5	0.0	86.2	100.0	7.9
Paper Birch*	BIRCH	5.9	15.5	0.0	0.0	18.8
Quaking Aspen*	ASPEN	7.0	0.0	0.0	0.0	0.0
Willow*	WILLOW	0.0	0.0	0.0	0.0	0.0
Balsam Poplar*	POPLAR	0.0	0.0	0.0	0.0	0.0
*Alnus incana**	INCANA	0.0	0.0	0.0	0.0	0.0
*Alnus crispa**	CRISPA	12.6	17.9	4.3	0.0	0.0
Tree/Tall Shrub Diversity (H')†	TSDIV	0.863	0.868	0.487	0.000	0.742
Stand Age (years)						
Mean Age	MAGE	166	160	154	56	124
Maximum Age	XAGE	200	185	250	65	190
Index of Heterogeneity (stems/DIST)††	SHET	28.6	27.9	20.4	44.1	27.7
Index of Heterogeneity (trees/TRDIST)††	THET	25.8	24.1	22.0	99.5	42.6

Table 2. Frequency of occurrence of plant species in understory and ground levels of each bird census plot, Tetlin-Northway study area, Alaska August 1977. Sample size is given in parentheses under each plot name.

	LOW AND MEDIUM SHRUB THICKETS (LMS)		TALL SHRUB THICKET (TS)			DECIDUOUS FOREST (DF)					MIXED DECIDUOUS-CONIFEROUS FOREST (MF)				CONIFEROUS FOREST (CF)			SCATTERED WOODLAND AND DWARF FOREST (WD)	
	Lowland Low & Medium Willow	Upland Low & Medium Willow	Lowland Tall Alder-Willow	Lowland Tall Willow-Poplar	Upland Tall Willow	Upland Aspen-Poplar	Upland Aspen #1	Upland Aspen #2	Upland Birch #1	Upland Birch #2	Upland Aspen-White Spruce	Upland Birch-White Spruce	Upland White Spruce-Aspen-Birch	Upland White Spruce-"Toothpick" Birch	Upland White Spruce #1	Upland White Spruce #2	Upland Black Spruce	Lowland White Spruce-Birch Woodland	Upland Black Spruce Bog
Sample Size	(38)	(14)	(32)	(14)	(14)	(14)	(98)	(14)	(98)	(14)	(16)	(98)	(20)	(14)	(98)	(14)	(14)	(14)	(14)
TREES																			
Betula papyrifera		50		21	7	14	20		83	71	13	80	30	79	17	43	7	14	
Picea glauca	21	14	34	85	71	29	26	7	9	29	75	62	55	86	96	100	7	86	
Picea mariana		7			7												100		100
Populus balsamifera	8		9	71		36	8	29	11		25		20						
Populus tremuloides			3			100	93	100	7		94		25	7	26				
TALL AND MEDIUM SHRUBS																			
Alnus crispa							1		54	36		51	45		27	57	43		
Alnus incana	5		94															7	
Betula glandulosa		14																	
Salix alaxensis			25	71														7	
Salix arbusculoides	3	38	34	64	43							1		7			7		14
Salix bebbiana		21	3	14	7	29	11	7	15	36	18	7	35	28					
Salix brachycarpa	5			36															35
Salix candida	34				21														
Salix glauca	21	71	6	71			3	7	1		13	1	10	14			29	28	7
Salix lanata richardsonii	11																		
Salix monticola	3			64	14							1							
Salix novae-angliae	97	28	34	64															
Salix planifolia pulchra	21	86	50	7	92												21	7	50
Salix scouleriana							1	29		21			10	21					
DWARF, LOW AND MEDIUM SHRUBS																			
Andromeda polifolia	3																		
Arctostaphylos rubra		36		42	50	36	8	7					10				50	64	93
Arctostaphylos uva-ursi	5		3	64			70	14			18			14	19			7	
Betula nana	100	79													1				
Chamaedaphne calyculata	3	21	18		57												7		64
Empetrum nigrum		7		7	21		14		3	7			20	7				100	50
Juniperus communis						7.1													
Ledum palustre	5	93	3	29	64	7.1	18		14	7	6	12	70		6		64	85	100
Linnaea borealis						92	89	93	84	71	75	22	35	100	57	42			14
Oxycoccus microcarpus																			93
Potentilla fruticosa	8	50	3		43						6								7
Rhododendron lapponicum		14																	

Table 2. (cont'd)

	LOW AND MEDIUM SHRUB THICKETS (LMS)		TALL SHRUB THICKET (TS)			DECIDUOUS FOREST (DF)					MIXED DECIDUOUS-CONIFEROUS FOREST (MF)				CONIFEROUS FOREST (CF)			SCATTERED WOODLAND AND DWARF FOREST (WD)	
	Lowland Low & Medium Willow	Upland Low & Medium Willow	Lowland Tall Alder-Willow	Lowland Tall Willow-Poplar	Upland Tall Willow	Upland Aspen-Poplar	Upland Aspen #1	Upland Aspen #2	Upland Birch #1	Upland Birch #2	Upland Aspen-White Spruce	Upland Birch-White Spruce	Upland White Spruce-Aspen-Birch	Upland White Spruce-"Toothpick" Birch	Upland White Spruce #1	Upland White Spruce #2	Upland Black Spruce	Lowland Spruce-Birch Woodland	Upland Black Spruce Bog
Ribes sp.			6		7				24	7		28			6				
Rosa acicularis	3		41	14		57	35	29	76	57	38	77	30	93	47	14	43	57	
Rubus idaeus									3							7			
Salix myrtillifolia	26				21													14	
Shepherdia canadensis				38		71	76	86		7	56		5	29	12				
Vaccinium uliginosum	18	29	22	7	14		8					1	10		1		86	86	100
Vaccinium vitis-idaea		21			79	35	68		18	7	13	15	85	14	91	29	100	100	100
Viburnum edule								43	19	21	6	1	5	43					
HERBS																			
Aconitum delphinifolium						43													
Amerorchis rotundifolia				17															
Anaphalis sp.	6																		
Anemone richardsonii												3			9				
Aster sp.	6														8				
Astragalus sp.				43															
Boschniakia rossica																			
Calla palustris	6		3																
Caltha palustris	6		9																
Castilleja caudata				7			1												
Corallorrhiza trifida															1				
Cornus canadensis															2				
Epilobium angustifolium		43	9	79	29	71	74	100	60	93	75	43	60	57	16	7			
Equisetum arvense					21		1			7		4	10		6		50		
Equisetum fluviatile	37		22		7														
Equisetum palustre	56																		
Equisetum pratense						7			50	7	6	71	60	7	42	64	36		
Equisetum scirpoides	34		47	50		21	72	57	55	57	44	33	65	50	45	36	86	21	79
Equisetum silvaticum			41			71									1		14		
Gentiana sp.	3																		
Geocaulon lividum			16		7	50	54	7	1		50	28	60	14	84	79	93	43	
Geum sp.																			
Goodyera repens															2				
Iris setosa			3																
Lupinus arcticus						100	33	64			31				26				
Lycopodium annotinum					7		2		4			4	10		2				
Mertensiana paniculata					29	93	55	79	83	100	63	48	40	86	20	43	36		7

	LOW AND MEDIUM SHRUB THICKETS (LMS)		TALL SHRUB THICKET (TS)			DECIDUOUS FOREST (DF)					MIXED DECIDUOUS-CONIFEROUS FOREST (MF)				CONIFEROUS FOREST (CF)			SCATTERED WOODLAND AND DWARF FOREST (WD)	
	Lowland Low & Medium Willow	Upland Low & Medium Willow	Lowland Tall Alder-Willow	Lowland Tall Willow-Poplar	Upland Tall Willow	Upland Aspen-Poplar	Upland Aspen #1	Upland Aspen #2	Upland Birch #1	Upland Birch #2	Upland Aspen-White Spruce	Upland Birch-White Spruce	Upland White Spruce-Aspen-Birch	Upland White Spruce-"Toothpick" Birch	Upland White Spruce #1	Upland White Spruce #2	Upland Black Spruce	Lowland Spruce-Birch Woodland	Upland Black Spruce Bog
Moneses uniflora									2						4	14	14		
Oxytropis campestris																		7	
Parnassia palustris	37			50														14	
Pedicularis labradorica	8		3				1		1						1			14	
Petasites hyperboreus				14	7				1						6		57		86
Polemonium acutiflorum						7	5	14	5		6	1							
Polygonum sp.		7																	
Potentilla palustris	5		34												1			7	
Pyrola asarifolia									5			2						21	
Pyrola chlorantha									10	7					1				
Pyrola grandiflora		36			8				1	7		2	10		5		7		50
Pyrola secunda				43		71	62	29	39		19	4	10	14	39	29	7		7
Pyrola sp.	21		47	14															
Rubus arcticus	84		81		29												14	7	14
Rubus chamaemorus		29			50										2		57		100
Rumex sp.	3														1			14	50
Saussurea angustifolia	11	7																	
Stellaria sp.									10	14	6	11			14		7	7	
Tofieldia pusilla	3																		
Valeriana capitata		7																	
Zygadenus elegans						7	3	21			31			7	10				
GRASSES AND SEDGES																			
Calamagrostis canadensis	13	100	63	79	79	100	60	43	84	64	81	80	65	14	84	57	86	86	43
Carex sp.	92	50	63	14	21	79	13	21	6	21			10	36	30		29	36	86
Eriophorum vaginatum	5	100			36													57	100

Table 5. Important correlation coefficients (r) between habitat and other variables and avian productivity and diversity variables, upper Tanana River Valley, Alaska, 1977. Statistical significance is indicated as * = $p \leq 0.05$ and ** = $p \leq 0.01$. Selected variables are from Table 1.

HABITAT VARIABLES	AVIAN COMMUNITY VARIABLES: Breeding Density	Species Diversity (H')	Breeding Biomass	Breeding Existence Energy (M)
Spatial Heterogeneity ~~(SHET)~~	0.310	0.189	0.585*	0.470*
Standing Water ~~(WATER)~~	0.419	0.384	0.755**	0.625**
Single-stemmedness ~~(SS)~~	-0.489*	-0.250	-0.349	-0.392
Multiple-stemmedness, small ~~(MSS)~~	0.487*	0.380	0.358	0.398
Distance between stems (~~DISTANCE~~)	0.380	0.306	0.609*	0.524*
Distance between trees (~~TRDISTANCE~~)	0.283	0.233	0.505*	0.420
% of Stems 4.7-10.0 m tall (HT)	-0.099	-0.378	-0.339	-0.234
% of Stems 2.5-4.6 m tall (HTS)	0.477*	0.351	0.488*	0.476*
% of Foliage >4. m high (FV4)	-0.488*	-0.259	-0.375	-0.425
Brush Density ≤1.0 m high (BRUSH)	0.523*	0.138	0.299	0.370
Tree/Shrub Density ≥2.54 cm dbh (TRDENS)	-0.552*	-0.396	-0.533*	-0.544*
Tall Shrub Density (DTS)	0.538*	0.358	0.481*	0.497*
Basal Area, Trees/Shrubs (BASAL)	-0.507*	-0.310	-0.485*	-0.512*
Willow Importance (WILLOW)	0.471*	0.058	0.203	0.303
Poplar Importance (POPLAR)	0.682**	0.419	0.541*	0.598**
Alnus incana Importance (INCANA)	0.415	0.388	0.772**	0.639**
OTHER VARIABLES				
Breeding Density-# Territories	--	0.739**	0.804**	0.915**
Breeding Biomass	0.804**	0.785**	--	0.965**

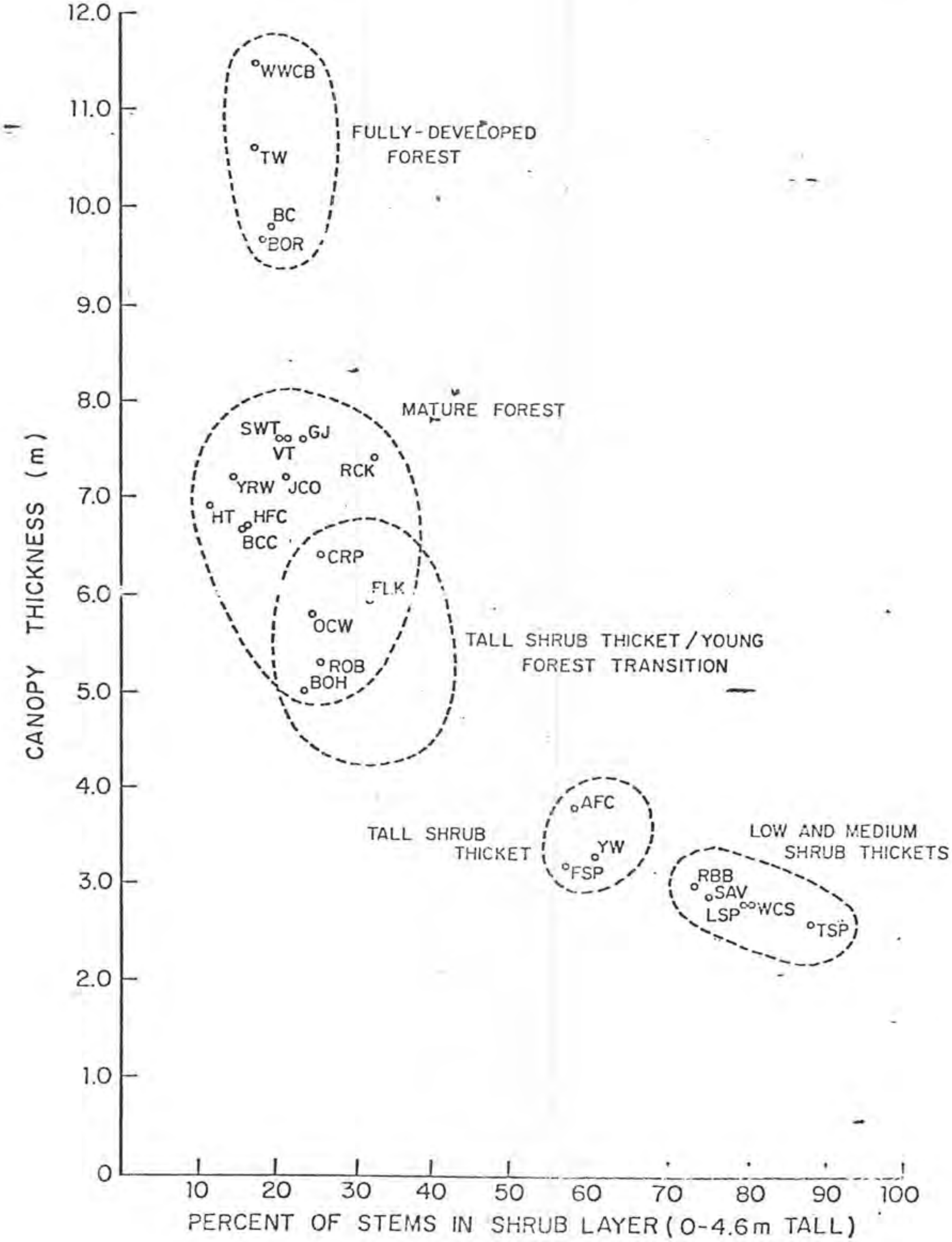

Figure 18. Ordination of 26 bird species from low shrub to fully-developed forest habitat, Tetlin-Northway study area, Alaska, 1977; based on their "mean habitat" relative to the habitat variables of canopy thickness and density of shrub stems.

APPENDIX

Appendix Table A-1. Summary of tree and shrub ages for the 18 Tetlin-Northway bird census plots. Based on increment borer samples taken August-November 1977.

Plot	Mean Age	Std Dev	Maximum Age	n
Lowland Low & Medium Willow Thickets	148.0	55.1	200	6
Upland Low & Medium Willow Thickets	44.4	10.0	60	9
Lowland Tall Alder-Willow Thicket	31.9	36.7	180	7
Lowland Tall Willow-Poplar Thicket	26.6	4.3	36	10
Upland Tall Willow Thicket	41.7	14.2	65	11
Upland Aspen-Poplar Forest	99.8	3.1	105	6
Upland Aspen Forest #1	36.3	7.4	107	14
Upland Aspen Forest #2	59.1	7.8	72	9
Upland Birch Forest #1	34.4	20.8	125	14
Upland Birch Forest #2	58.1	9.1	76	10
Upland Aspen-White Spruce Forest	63.1	11.0	80	11
Upland Birch-White Spruce Forest (E-side)	105.6	16.9	130	7
Upland Birch-White Spruce Forest (W-side)	56.5	4.7	60	7
Upland White Spruce-Aspen-Birch Forest	53.5	5.7	57	4
Upland White Spruce-"Toothpick" Birch Forest	49.9	5.3	75	8
Upland White Spruce Forest #1	165.5	16.9	200	15
Upland White Spruce Forest #2	159.6	15.3	185	7
Upland White Spruce Forest	153.6	51.5	250	7
Lowland White Spruce-Birch Woodland	124.0	66.6	190	5
Upland Black Spruce Bog	56.3	6.6	65	7

Appendix Table A-2. Weights of common interior Alaska breeding birds, obtained from University of Alaska Museum specimens collected during the breeding season, from West and DeWolfe (1974, Table 5) and from calculations based on Carbyn (1971, Table 1).

Species	Weight (g)	Source
Mallard	1117.8	UAM (Univ. Alaska Museum)
Pintail	856.1	UAM
Green-winged Teal	336.8	UAM
American Wigeon	815.6	UAM (905.2), LSU (726.0)
Northern Shoveler	609.9	UAM (775.7), LSU (444.0)
Sharp-shinned Hawk	160.0	UAM
American Kestrel	124.5	UAM
Spruce Grouse	561.2	UAM
Ruffed Grouse	593.6	UAM
Sandhill Crane	2481.0	UAM
Common Snipe	97.3	UAM
Solitary Sandpiper	51.5	UAM
Lesser Yellowlegs	80.5	UAM
Northern Phalarope	33.4	UAM
Mew Gull	432.8	UAM
Great Horned Owl	1416.5	UAM
Hawk Owl	341.7	UAM
Common Flicker	177.0	UAM
Hairy Woodpecker	74.0	UAM
Downy Woodpecker	25.8	UAM
Northern Three-toed Woodpecker	56.9	UAM
Alder Flycatcher	12.6	UAM (12.3), Carbyn (12.0) West & DeWolfe (13.6)
Hammond's Flycatcher	11.0	UAM
Olive-sided Flycatcher	34.1	UAM
Tree Swallow	18.0	UAM (18.4), LSU (17.6)

Appendix Table A-2. (cont'd)

Species	Weight (g)	Source
Bank Swallow	17.3	UAM
Cliff Swallow	18.3	UAM
Gray Jay	72.3	UAM
Black-capped Chickadee	11.7	UAM
Boreal Chickadee	11.5	UAM (12.1), Carbyn (11.0)
Brown Creeper	7.8	UAM
American Robin	88.0	UAM, Carbyn (88.0)
Varied Thrush	78.5	UAM
Swainson's Thrush	28.0	UAM (27.4), West & DeWolfe (26.8), Carbyn (31.0)
Hermit Thrush	27.0	UAM
Gray-checked Thrush	29.5	UAM (30.1), Carbyn (29.0)
Ruby-crowned Kinglet	7.0	UAM (6.3), Carbyn (8.0), West & DeWolfe (6.6)
Bohemian Waxwing	59.3	UAM (60.6), Carbyn (58.0)
Orange-crowned Warbler	9.5	UAM (9.8), West & DeWolfe (8.3)
Yellow Warbler	9.7	UAM (10.0), West & DeWolfe (9.4)
Yellow-rumped Warbler	12.5	UAM (13.0), West & DeWolfe (12.3), Carbyn (12.0)
Townsend's Warbler	9.4	UAM
Blackpoll Warbler	12.4	UAM (12.8), Carbyn (12.0)
Northern Waterthrush	17.3	UAM (17.0), LSU (17.6)
Wilson's Warbler	7.7	UAM (7.8), West & DeWolfe (7.6)
Rusty Blackbird	48.9	UAM
Pine Grosbeak	59.7	UAM
Common Redpoll	14.2	UAM
Pine Siskin	12.2	UAM
White-winged Crossbill	24.4	UAM
Savannah Sparrow	18.0	UAM
Dark-eyed Junco	18.6	UAM (18.4), West & DeWolfe (18.5), Carbyn (19.0)

Appendix Table A-2. (cont'd)

Species	Weight (g)	Source
Tree Sparrow	17.9	UAM
White-crowned Sparrow	24.0	UAM (23.7), West & DeWolfe (25.0)
Fox Sparrow	36.6	
Lincoln's Sparrow	15.8	UAM (15.7), Carbyn (16.0)

Appendix Table A-3. Chronology of six months of field work, 1977, Tetlin Junction-Northway study area, Alaska.

17 May	Commenced field work, most trees and shrubs not yet green Larger lakes still ice-covered, rivers and ponds ice-free
18 May	Selected potential bird census plot locations
21 May	Began surveying census plots
28 May	Began censusing plots Most tree, shrub, and herbaceous vegetation had green foliage
2 June	Dark-eyed Junco nest with eggs White-crowned Sparrow nest with eggs Tree Sparrow nest with eggs
4 June	First Fox Sparrow fledglings Lesser Yellowlegs nest with eggs
6 June	Orange-crowned Warbler nest with eggs
10 June	Hatching Dark-eyed Junco
13 June	Boreal Chickadee observed feeding young, still in nest cavity Black-capped Chickadee adult observed entering nest cavity
14 June	Pintail nest with eggs First Dark-eyed Junco fledgling
15 June	First hatching Lesser Yellowlegs First Rusty Blackbird fledgling Common Flicker nest with eggs First hatching Orange-crowned Warbler
16 June	First Varied Thrush fledgling First brood of Lesser Scaup
19 June	First Tree Sparrow fledglings
21 June	First Hermit Thrush nest with eggs
25 June	Mallard brood First hatched Yellow Warbler
26 June	Alder Flycatcher nest with eggs

Appendix Table A-3. (cont'd)

27 June	First Orange-crowned Warbler fledglings Horned Grebe nest with eggs
28 June	First Swainson's Thrush fledglings Pintail brood
29 June	First Savannah Sparrow fledglings First Ruffed Grouse young out of nest
2 July	First Bohemian Waxwing fledglings
4 July	First Yellow-rumped Warbler fledgling First brood Green-winged Teal
5 July	First flight-capable immature Sandhill Cranes
6 July	First Red-necked Grebe brood First Northern Shoveler brood First Bufflehead brood First Horned Grebe brood Flightless, molting adult Mallard seen First Canvasback brood seen
7 July	Juvenal Gray Jay molting to first winter plumage Gray Jay family groups dispersing; young independent First Brown Creeper fledglings
8 July	Boreal Chickadee fledgling First Townsend's Warbler fledgling First Arctic Loon young First Greater Scaup brood First Common Goldeneye brood First Bonaparte's Gull young First Arctic Tern young
10 July	American Wigeon brood First flight-capable Lesser Yellowlegs young
13 July	Ruby-crowned Kinglet fledglings
17 July	Rusty Blackbird adults molting to fall plumage First White-winged Scoter brood
18 July	Cliff Swallows feeding young
23 July	Semipalmated Plover young

Appendix Table A-3. (cont'd)

24 July	First fall migrant--Baird's Sandpiper, Least Sandpiper First flightless adult and immature Canada Geese First Whistling Swan--lone straggler
25 July	First flight-capable immature Common Snipe
27 July	First Blue-winged Teal brood
2 Aug	Last Olive-sided Flycatcher
10 Aug	Last Mew Gull
14 Aug	Last Hammond's Flycatcher Last Townsend's Warbler
16 Aug	Last Alder Flycatcher Last Cliff Swallow
18 Aug	Last Solitary Sandpiper
21 Aug	Last Spotted Sandpiper Last Bank Swallow
24 Aug	Last Orange-crowned Warbler
1 Sept	Last Common Flicker
2 Sept	Last Sharp-shinned Hawk
3 Sept	Last Brown Creeper
10 Sept	Last Belted Kingfisher
11 Sept	Last Arctic Loon Last White-fronted Goose Last Green-winged Teal
12 Sept	Last Hermit Thrush Last Northern Shrike
16 Sept	Last Red-necked Grebe Last Horned Grebe Last Pintail Last American Wigeon

Appendix Table A-3. (cont'd)

16 Sept	Last Northern Shoveler Last Canvasback Last Lesser Scaup Last Bufflehead
18 Sept	Last Common Snipe Last Swainson's Thrush Last Yellow-rumped Warbler Last Wilson's Warbler
19 Sept	First snowfall at Riverside Lodge Last Common Goldeneye Last Blue-winged Teal Last American Kestrel
21 Sept	Height of autumn foliage color on deciduous trees
22 Sept	Last Merlin Last Peregrine Falcon
23 Sept	Last Bald Eagle Last Varied Thrush Last Ruby-crowned Kinglet Last Water Pipit Last White-crowned Sparrow
27 Sept	Last Sandhill Crane Last Pine Siskin Last Fox Sparrow
1 Oct	Most leaves off deciduous trees and shrubs Last Golden Eagle
8 Oct	Last Marsh Hawk
13 Oct	Last Rusty Blackbird
14 Oct	Last Canada Goose
17 Oct	Last Whistling Swan
18 Oct	First heavy snowfall (= 10 cm), first lasting snow cover Tanana River frozen completely Last Red-breasted Merganser
19 Oct	Last Rough-legged Hawk

Appendix Table A-3. (cont'd)

27 Oct	Last Tree Sparrow
28 Oct	Last Starling First Black-billed Magpie
29 Oct	Last Dark-eyed Junco
30 Oct	Last American Robin
3 Nov	Last observation of waterfowl--3 Mallards on Tanana River
4 Nov	Last Snow Buntings
13 Nov	Depart Riverside Lodge Field Station

Appendix Table A-4. Bird nests found in Tetlin Junction-Northway study area, 1977.

Species	Date Found	No. Eggs/Young	Status	Hatching Date	Fledging Date	Habitat
Dark-eyed Junco	2 June	5	incubating		16 June	ground, under *Ledum* bush, Birch-White Spruce forest
White-crowned Sparrow	2 June	5	incubating	11 June		ground, in sedge tussock, under *Betula nana*, Low-Medium willow shrub
Tree Sparrow	2 June	5	incubating	12 June	19 June	ground, in base of *Salix novae-angliae* bush, Low-Medium willow shrub
Lesser Yellowlegs	4 June	4	incubating	15 June		ground, at base of *Salix novae-angliae* bush, Low-Medium willow shrub
Dark-eyed Junco	10 June	4	hatched			ground, under grass tussock, Aspen-Poplar forest
Pintail	13 June	5	incubating			ground, steep gravel berm of Alaska Highway, 10 m from highway, near sedge wetlands
Black-capped Chickadee	13 June					6 m high in rotted Paper Birch trunk, Paper Birch forest
Boreal Chickadee	13 June		hatched			8 m high in rotted Paper Birch trunk, Paper Birch forest
Common Flicker	15 June	?	incubating	26 June		3 m high in rotted Balsam Poplar trunk, Tall Willow shrub
Orange-crowned Warbler	6 June	4	incubating	15 June	27 June	ground, under *Viburnum edule* bush, in grass clump, open Paper Birch-White Spruce forest
Hermit Thrush	21 June	4	incubating	2 July	12 July	ground, under White Spruce re-growth in open field, surrounded by White Spruce-Aspen forest
Yellow Warbler	25 June	4	brooding		29 June	2 m high in *Salix arbusculoides* bush in open Tall Willow stand
Yellow Warbler	26 June	4	brooding		30 June	3 m high in *Salix arbusculoides* bush in dense Tall Willow/Alder stand
Alder Flycatcher	26 June	4	incubating			1 m high in *Alnus crispa* growing in standing water, Tall Willow/Alder stand
Horned Grebe	27 June	3	incubating	6 July		ground, *Equisetum fluviatile* island at pond edge
Hermit Thrush	30 June	4	incubating	8 July		ground, surrounded by *Epilobium angustifolium* and *Calamagrostis canadensis*, in Paper Birch forest
Dark-eyed Junco	1 July	4	incubating	7 July		ground, under grass clump in open White Spruce regrowth, surrounded by mature White Spruce forest
White-crowned Sparrow	5 July	4	incubating			ground, at base of *Betula nana*, Low-Medium willow shrub
Orange-crowned Warbler	9 July	3	incubating			ground, in grass clump in open, young Aspen stand
Red-necked Grebe	7 July	3	incubating			on floating *Nuphar polysepalum* (Pond Lily) in shallow pond
Lesser Scaup	10 July	8	incubating			in sedge marsh, atop tussock, 1 m from pond edge, 0.25 m above water level

Appendix Table A-5. Climatic characteristics at Northway, Alaska, May-September 1977. (Source: U.S. NOAA 1977)

	May	June	July	August	September	October
Temperature						
Mean maximum temperature (°F)	55.9	65.7	70.4	72.2	53.5	29.9
Mean minimum temperature (°F)	33.3	43.5	46.2	45.5	32.3	13.5
Mean temperature (°F)	44.6	54.6	58.3	58.9	42.9	21.7
Departure from normal (°F)	+0.2	-1.3	-0.2	+5.3	+1.1	-0.1
Precipitation						
Total (inches)	1.98	2.14	0.97	0.62	1.51	0.29
Departure from normal (inches)	+1.18	+0.24	-1.56	-1.02	+0.39	-0.24
Number of days with >0.10 inches	9	8	3	3	1	0
Day of greatest precipitation	5/26	6/21	7/15	8/26	9/22	10/18
(Inches on that day)	0.45	0.50	0.35	0.25	1.12	0.70

Appendix Table A-6. Breeding bird density and presence of non-breeding birds on 24 census plots, Tanana River Valley, Alaska. Breeding densities are expressed in numbers of territories/10 ha and are based on six to eight censuses on each plot during the breeding season (May-June). Plot sizes varied from 1.61 to 10.0 ha. Fairbanks plots (F) were censused in 1975; Tetlin Junction (T), Riverside Lodge (R), and Northway (N) plots were censused in 1977. Key: + = small portion of a breeding territory on census plot, counted as 0.1 in density and diversity calculations; v = a non-breeding visitor to plot; * = deletion from biomass and exist energy calculations, because of disproportionate influence caused by family of heavy-bodied birds.

	LOW AND MEDIUM SHRUB THICKETS		
Plot:	Lowland Low & Med Willow	Upland Low & Med Willow	Lowland Tussock-Low & Med Shrub Bog
Location:	N	R	F
Species / Size (ha):	4.25	1.61	10.00
Mallard	+		
Pintail			
Green-winged Teal	+		
Sharp-shinned Hawk			
American Kestrel			
Spruce Grouse			
Ruffed Grouse			
Sandhill Crane			+
Common Snipe	8.2	0.5	2.0
Solitary Sandpiper	v		
Lesser Yellowlegs	4.7		
Great Horned Owl			
Hawk Owl	v		
Common Flicker	+		v
Hairy Woodpecker			
Northern Three-toed Woodpecker			
Alder Flycatcher	+		1.0
Hammond's Flycatcher		v	
Olive-sided Flycatcher			
Violet-green/Tree Swallow	v		v
Bank Swallow	v		
Cliff Swallow	v		
Gray Jay		v	
Black-capped Chickadee			
Boreal Chickadee			
Brown Creeper			
American Robin	1.2	2.3	v
Varied Thrush			
Hermit Thrush			
Swainson's Thrush	+		v
Gray-cheeked Thrush	v	0.5	
Ruby-crowned Kinglet	v		
Bohemian Waxwing	v	v	v
Orange-crowned Warbler	+	2.3	2.0
Yellow Warbler	1.2		
Yellow-rumped Warbler			
Townsend's Warbler			
Blackpoll Warbler			
Northern Waterthrush			
Wilson's Warbler			
Rusty Blackbird	2.4		v
Pine Grosbeak	v	v	
Common Redpoll	v	0.5	v
Pine Siskin			
White-winged Crossbill			
Savannah Sparrow	3.5		v
Dark-eyed Junco		2.3	v
Tree Sparrow	4.7		5.0
White-crowned Sparrow	9.4	10.0	5.5
Fox Sparrow	v		
Lincoln's Sparrow	8.2	9.3	8.0
Total Density (territories/10 ha)	44.1	27.7	23.6
Total Biomass (g/10 ha)	4050	1452	1198
Total Existence Energy (k cal/10 ha)	1518	635	516
Total Species; Breeding Species	26;15	12;8	16;7
Species Diversity (H')	2.071	1.587	1.610
Species Evenness (J')	0.785	0.763	0.828
Dominance (%)	39.9	71.0	57.2

Appendix Table A-6. (cont'd)

		TALL SHRUB THICKET			
	Plot:	Lowland Tall Alder-Willow	Lowland Tall Willow-Poplar	Upland Tall Willow	Lowland Tall Alder-Willow
	Location:	N	N	R	F
Species	Size (ha):	3.35	1.61	1.61	10.00
Mallard		+			v
Pintail					1.0
Green-winged Teal		+			2.0
Sharp-shinned Hawk					
American Kestrel					
Spruce Grouse					
Ruffed Grouse					
Sandhill Crane					
Common Snipe		1.5			7.5
Solitary Sandpiper		v	v		2.0
Lesser Yellowlegs		3.0	0.4		2.0
Great Horned Owl					
Hawk Owl		v			
Common Flicker		1.0		0.5	v
Hairy Woodpecker					
Northern Three-toed Woodpecker					
Alder Flycatcher		10.5	9.8	9.6	1.5
Hammond's Flycatcher					v
Olive-sided Flycatcher					
Violet-green/Tree Swallow					v
Bank Swallow					
Cliff Swallow		v			
Gray Jay		+	v	v	v
Black-capped Chickadee					v
Boreal Chickadee		v	v	—	v
Brown Creeper					
American Robin		1.5	0.4	2.4	v
Varied Thrush					
Hermit Thrush					
Swainson's Thrush		4.2	v	4.8	1.0
Gray-cheeked Thrush		+	+		4.0
Ruby-crowned Kinglet		v			v
Bohemian Waxwing		v			v
Orange-crowned Warbler		6.0	7.9	9.6	v
Yellow Warbler		16.4	15.7		10.0
Yellow-rumped Warbler		v			v
Townsend's Warbler					
Blackpoll Warbler					3.0
Northern Waterthrush		4.8			4.5
Wilson's Warbler					
Rusty Blackbird		3.0	v		1.0
Pine Grosbeak		v			v
Common Redpoll		v	3.9		+
Pine Siskin					
White-winged Crossbill			v		
Savannah Sparrow		v	11.8		v
Dark-eyed Junco		v		9.6	2.0
Tree Sparrow		1.5			6.0
White-crowned Sparrow		3.0	7.9	4.8	1.0
Fox Sparrow		3.0	5.9		3.0
Lincoln's Sparrow		4.5	3.9	0.5	6.5
Total Density (territories/10 ha)		64.3	67.7	41.8	58.1
Total Biomass (g/10 ha)		3544	2176	1896	5608
Total Existence Energy (k cal/10 ha)		1464	1141	847	1968
Total Species; Breeding Species		29;18	17;11	9;8	32;18
Species Diversity (H')		2.364	2.036	1.781	2.584
Species Evenness (J')		0.818	0.849	0.856	0.894
Dominance (%)		41.8	40.6	45.9	30.1

Appendix Table A-6. (cont'd)

Species	DECIDUOUS FOREST				
Plot:	Upland Aspen-Poplar	Upland Aspen #1	Upland Aspen #2	Upland Birch #1	Upland Birch #2
Location:	R	R	N	R	R
Size (ha):	1.61	10.00	1.61	10.00	1.61
Mallard					
Pintail					
Green-winged Teal					
Sharp-shinned Hawk				+	
American Kestrel					
Spruce Grouse					
Ruffed Grouse		+		+	
Sandhill Crane					
Common Snipe					
Solitary Sandpiper					
Lesser Yellowlegs					
Great Horned Owl					0.3*
Hawk Owl					
Common Flicker	0.3	+			
Hairy Woodpecker					
Northern Three-toed Woodpecker					
Alder Flycatcher	1.3		0.4	+	
Hammond's Flycatcher	3.8	+		+	v
Olive-sided Flycatcher					
Violet-green/Tree Swallow					
Bank Swallow					
Cliff Swallow					
Gray Jay		0.5	0.4	1.0	v
Black-capped Chickadee	0.3	+	v	1.0	
Boreal Chickadee		v		0.5	
Brown Creeper					
American Robin	3.1	6.5	4.9	0.5	1.6
Varied Thrush		v	v	1.0	v
Hermit Thrush	2.6	+	6.1	1.0	3.3
Swainson's Thrush	3.8	4.5	0.4	5.5	6.6
Gray-cheeked Thrush					
Ruby-crowned Kinglet					
Bohemian Waxwing		+			
Orange-crowned Warbler	5.1	5.5	4.1	4.5	3.0
Yellow Warbler		v			
Yellow-rumped Warbler	3.3	6.0	5.3	5.0	6.6
Townsend's Warbler		v			
Blackpoll Warbler					
Northern Waterthrush					
Wilson's Warbler		v			
Rusty Blackbird				v	
Pine Grosbeak		v		v	
Common Redpoll		+		1.0	
Pine Siskin					
White-winged Crossbill					
Savannah Sparrow					
Dark-eyed Junco	5.1	4.0	5.3	5.5	4.3
Tree Sparrow					
White-crowned Sparrow					
Fox Sparrow					
Lincoln's Sparrow					
Total Density (territories/10 ha)	28.7	27.7	26.9	26.9	25.7
Total Biomass (g/10 ha)	1498	2058	1690	1386	1212
Total Existence Energy (k cal/10 ha)	642	792	700	592	546
Total Species; Breeding Species	10;10	19;13	10;8	17;15	10;7
Species Diversity (H')	2.092	1.782	1.761	2.104	1.736
Species Evenness (J')	0.908	0.695	0.847	0.777	0.892
Dominance (%)	35.5	45.1	42.4	40.9	43.2

Appendix Table A-6. (cont'd)

Species	Plot:	Upland Aspen-White Spruce	Upland Birch-White Spruce	Upland White Spruce-Aspen-Birch	Lowland White Spruce-Black Spruce-Birch	Upland White Spruce-"Toothpick" Birch
		MIXED DECIDUOUS-CONIFEROUS FOREST				
	Location:	N	N	R	F	N
	Size (ha):	1.84	10.00	2.20	10.00	1.61
Mallard						
Pintail						
Green-winged Teal						
Sharp-shinned Hawk			+			v
American Kestrel					v	
Spruce Grouse						
Ruffed Grouse			+			
Sandhill Crane						
Common Snipe					2.0	
Solitary Sandpiper					v	
Lesser Yellowlegs					v	
Great Horned Owl						
Hawk Owl						
Common Flicker			v		v	
Hairy Woodpecker						
Northern Three-toed Woodpecker						
Alder Flycatcher					+	
Hammond's Flycatcher						
Olive-sided Flycatcher					0.5	
Violet-green/Tree Swallow					v	
Bank Swallow						
Cliff Swallow						
Gray Jay		0.4	1.0	1.5	0.5	v
Black-capped Chickadee					+	
Boreal Chickadee		1.3	+	1.5	1.0	
Brown Creeper			1.0			
American Robin		2.2	1.0	3.0	+	
Varied Thrush		0.4	2.0	v	+	
Hermit Thrush		2.2				
Swainson's Thrush		10.8	11.0	5.9	5.0	
Gray-cheeked Thrush					0.5	
Ruby-crowned Kinglet		2.2	+	3.0	1.0	
Bohemian Waxwing			v		v	
Orange-crowned Warbler		4.4	1.5	3.9	+	
Yellow Warbler						
Yellow-rumped Warbler		2.2	6.5	5.9	4.5	
Townsend's Warbler			5.0			
Blackpoll Warbler						
Northern Waterthrush					2.0	
Wilson's Warbler			v		v	
Rusty Blackbird					+	
Pine Grosbeak			v		0.5	v
Common Redpoll		1.0	1.0		0.5	
Pine Siskin						
White-winged Crossbill		v	v			
Savannah Sparrow						
Dark-eyed Junco		8.8	6.0	6.9	7.0	
Tree Sparrow					v	
White-crowned Sparrow					1.0	
Fox Sparrow					2.0	
Lincoln's Sparrow					v	
Total Density (territories/10 ha)		35.9	36.4	31.6	28.6	0
Total Biomass (g/10 ha)		1786	1958	1630	1602	0
Total Existence Energy (k cal/10 ha)		794	832	703	689	0
Total Species; Breeding Species		12;11	19;14	9;8	29;20	3;0
Species Diversity (H')		1.968	1.990	1.954	2.323	0
Species Evenness (J')		0.821	0.754	0.939	0.775	0
Dominance (%)		54.6	48.1	40.5	42.0	0

Appendix Table A-6. (cont'd)

	CONIFEROUS FOREST			
Plot:	Upland White Spruce #1	Upland White Spruce #2	Upland Black Spruce	Lowland Black Spruce
Location:	T	T	T	F
Species / Size (ha):	10.00	1.61	1.61	5.75
Mallard				
Pintail				
Green-winged Teal				
Sharp-shinned Hawk	+			
American Kestrel	+			
Spruce Grouse			0.5*	
Ruffed Grouse	+		v	
Sandhill Crane				
Common Snipe				1.7
Solitary Sandpiper				v
Lesser Yellowlegs				0.2
Great Horned Owl	+	+		
Hawk Owl				
Common Flicker	v			
Hairy Woodpecker	+			
Northern Three-toed Woodpecker	+		+	
Alder Flycatcher				
Hammond's Flycatcher				
Olive-sided Flycatcher				v
Violet-green/Tree Swallow				
Bank Swallow				
Cliff Swallow				
Gray Jay	1.0	0.5	1.0	0.2
Black-capped Chickadee				
Boreal Chickadee	2.0	+	1.0	
Brown Creeper	1.5			
American Robin				0.2
Varied Thrush	+			
Hermit Thrush		2.5		
Swainson's Thrush	7.0	5.1	3.6	
Gray-cheeked Thrush			+	2.6
Ruby-crowned Kinglet	+		2.0	0.9
Bohemian Waxwing	v			1.7
Orange-crowned Warbler				
Yellow Warbler				
Yellow-rumped Warbler	1.5			3.1
Townsend's Warbler	9.5	10.0		
Blackpoll Warbler				
Northern Waterthrush				
Wilson's Warbler				
Rusty Blackbird				v
Pine Grosbeak	v			
Common Redpoll	+			0.2
Pine Siskin	v			
White-winged Crossbill	v	v	v	
Savannah Sparrow				v
Dark-eyed Junco	3.5	3.0	7.2	7.8
Tree Sparrow				
White-crowned Sparrow				3.5
Fox Sparrow				v
Lincoln's Sparrow				v
Total Density (territories/10 ha)	26.9	21.3	15.5	22.1
Total Biomass (g/10 ha)	1450	1080	682	1328
Total Existence Energy (k cal/10 ha)	566	432	312	563
Total Species; Breeding Species	21;16	8;7	10;8	17;11
Species Diversity (H')	1.808	1.363	1.489	1.882
Species Evenness (J')	0.652	0.701	0.716	0.785
Dominance (%)	48.3	70.9	69.7	51.1

Appendix Table A-6. (cont'd)

Species	Plot:	Lowland White Spruce-Birch Woodland	Upland Black Spruce Bog	Lowland Black Spruce Bog
		SCATTERED WOODLAND AND DWARF FOREST		
	Location:	N	R	F
	Size (ha):	1.61	1.61	4.25
Mallard				
Pintail				
Green-winged Teal				
Sharp-shinned Hawk				
American Kestrel				
Spruce Grouse				
Ruffed Grouse				
Sandhill Crane				
Common Snipe				1.2
Solitary Sandpiper				v
Lesser Yellowlegs		0.3		2.3
Great Horned Owl				
Hawk Owl				
Common Flicker		+		
Hairy Woodpecker				
Northern Three-toed Woodpecker				
Alder Flycatcher			v	
Hammond's Flycatcher				
Olive-sided Flycatcher			0.3	
Violet-green/Tree Swallow				
Bank Swallow				
Cliff Swallow				
Gray Jay		v	0.3	+
Black-capped Chickadee				
Boreal Chickadee				
Brown Creeper				
American Robin		3.4	1.7	0.2
Varied Thrush			v	
Hermit Thrush				
Swainson's Thrush		v	5.0	
Gray-cheeked Thrush		3.4		2.3
Ruby-crowned Kinglet		3.4	3.3	
Bohemian Waxwing		v		+
Orange-crowned Warbler		3.4	1.7	
Yellow Warbler		1.7		
Yellow-rumped Warbler				0.5
Townsend's Warbler				
Blackpoll Warbler				
Northern Waterthrush				
Wilson's Warbler				
Rusty Blackbird		3.4		
Pine Grosbeak				
Common Redpoll				+
Pine Siskin				
White-winged Crossbill				
Savannah Sparrow				v
Dark-eyed Junco		3.4	6.6	8.2
Tree Sparrow			v	
White-crowned Sparrow		8.4	3.3	5.9
Fox Sparrow		3.0		
Lincoln's Sparrow		3.4		
Total Density (territories/10 ha)		37.3	22.2	20.9
Total Biomass (g/10 ha)		2218	1126	1404
Total Existence Energy (k cal/10 ha)		937	496	581
Total Species; Breeding Species		15;12	11;8	12;10
Species Diversity (H')		2.262	1.773	1.534
Species Evenness (J')		0.916	0.853	0.698
Dominance (%)		31.6	52.3	67.5