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Breeding bird diversity in Douglas-fir stands of western Montana as related to forest structure

Garet Peter Munger

The University of Montana

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BREEDING BIRD DIVERSITY IN DOUGLAS-FIR
STANDS OF WESTERN MONTANA AS RELATED
TO FOREST STRUCTURE

By
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B.A., The College of Wooster, 1966

Presented in partial fulfillment of the requirements for the
degree Master of Science: Resource Conservation

University of Montana
School of Forestry

1974

Approved by:

[Signatures]

Chairman, Board of Examiners

Dean, Graduate School

Date: June 25, 1974
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I wish also to acknowledge the support and encouragement of the members of my graduate committee; Larry Forcier, Sid Frissell, Arnold Bolle and Andrew Sheldon, who assured me that even if the project did not turn out as anticipated, something surely could be salvaged for a Master's thesis. Special thanks to Larry Forcier as chairman of the committee for his considerable assistance in the writing of this thesis.
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CHAPTER I

INTRODUCTION

Species diversity is a concept which has long been assumed to have biological significance and has been considered to be an important parameter in describing ecosystems. Interest in species diversity has arisen from investigation of two related subjects, the mechanisms limiting the number of species which can coexist in a given area and from the concept that there is a positive relationship between species diversity and community stability. In addition, there is an increasing awareness of diversity as an aesthetic value. Pimlott (1969) argued for the recognition of diversity of habitats as a positive value in wildlife management and other land management activities. The present study, an investigation of the role of forest structure in limiting the number of coexisting bird species was suggested by the hypothesis that (1) changes in the structure of forest stands as a result of management activities will affect the kinds and numbers of birds which can be supported and (2) that such changes in the bird community will alter ecosystem stability relationships by changing the effect the bird community can have on community events such as insect population outbreaks.

That birds do make a significant contribution to the control of insect populations was suggested by Bruns (1960), Tinbergen (1960), Morris (1963) and Dowden and Carolin (1950). These authors indicated
that the bird community can consume a significant proportion of endemic insect populations. However, birds are apparently ineffective in reducing epidemic insect population levels. The potential of birds in contributing to insect control is especially recognized in Europe where there have been a number of studies attempting to increase bird populations by installing suitable nest boxes in forest stands.

In England and Europe where more intensive forestry is practiced there is concern about changes in bird habitat due to forest management activities. Williamson (1972) has expressed this concern in the observation that conversion of large areas of English forests to faster growing conifers is resulting in the decline of many native bird populations. While it seems unlikely that the generally extensive forest management practices in western Montana will have effects on the bird community of the magnitude observed in Europe, it is important to assess the relationship of the bird community with the total ecosystem because of the presumed and logical relationship between species diversity and community stability.

That there is a positive relationship between species diversity and stability has become almost a part of ecological dogma supported largely by an accumulation of natural historical examples. Elton (1958 and 1966) has collected an array of these examples and developed an argument for the complexity stability theory based largely on comparisons of natural and agricultural ecosystems. For instance, it has always seemed apparent that areas of high species diversity such as coral reefs and tropical rain forests are highly stable and that agricultural monocultures are unstable. However, there are some
apparently contradictory examples. Tidal flats are characterized as being quite stable but are low in species diversity, and Watt (1968) has made the observation that "it is a fact that many of the most historically important species (rodents, locusts, grasshoppers, and forest-insect defoliators such as the spruce budworm) are attacked by an enormous variety of species".

There have been relatively few field studies which illustrate the diversity-stability relationship, though one by Pimentel (1961) showed that insect population outbreaks were reduced in fields having greater plant diversity. Flaherty (1969) similarly found that a predatory mite was better able to regulate the Willamette mite, a pest of California grapes, when weedy grasses were associated with the grapevines than when the weeds were eliminated. Presumably the greater effectiveness of the predatory mite population was due to the maintenance of alternate prey in the more diverse vegetational pattern provided by the interspersion of weedy grasses among the vines.

In 1955, R. H. MacArthur introduced a degree of formality to the diversity-stability dogma by suggesting that the degree of community stability might be approximately proportional to the logarithm of the number of links in a food chain. This logarithm measures the degree of complexity of the food chain, and ecological intuition leads to its association with community stability. In spite of the accumulation of natural historical evidence and MacArthur's contribution, almost all of the experimental and theoretical modeling studies seem to indicate that as a mathematical generality, increased species diversity and complexity is associated with decreased community stabil-
ity (May, 1973).

The diversity-stability relationship is obviously not simple, especially when comparisons of disturbed and natural communities are being made. It seems plausible that natural communities, because they are the result of a long history of coevolution, can be stable whether they are structurally complex or simple, whereas the investigations of Pimentel and Flaherty suggest that in disturbed communities, stability can be enhanced by structural complexity.

Past Research.

Unlike some groups such as insects and plants in which community diversity seems to be self-augmenting, environmental structure places an upper limit on bird diversity (Whittaker, 1970) and provides the framework within which the environmental hyperspace (Hutchinson, 1957) can be partitioned into bird niches (MacArthur, 1972). In the case of forest birds the distribution of foliage, as might be described in a vertical foliage profile, provides the framework for the bird community. Lack (1933) alluded to this idea in his study of the effect of afforestation of grassland and heath in England when he concluded that the birds were more affected by changes in the height of vegetation than by its species composition. MacArthur and MacArthur (1961) further developed and quantified this relationship of structure and bird diversity. They found that an adequate description of the vegetational structure is provided by the foliage height diversity (FHD). FHD is a measure of the evenness of the distribution of foliage in layers from the ground level to the top of the canopy. Areas where
the forest is tallest and where the foliage is evenly distributed at all levels will have a high FHD. In contrast, shorter forest stands and ones in which the foliage is less evenly distributed have a lower FHD. Because FHD provides a measure of the structural development and complexity of the stand, areas with high FHD values can be predicted to support a more diverse bird community than areas with lower FHD values. The MacArthurs developed their measure of FHD over a series of study areas in the eastern United States and found a high correlation between FHD and bird species diversity (BSD). In this original study they measured foliage densities at 0.5, 2, 5, 10, 20, 30, 45, and 60 ft, and used these values to construct a foliage profile. They then divided the foliage into several different arrangements of layers to calculate FHD values using the Shannon-Weaver (Pielou, 1966 e.g.) index of diversity. When the layers were identified as 0-2 ft, 2-25 ft, and above 25 ft and BSD was plotted against FHD, a good correlation was obtained (Figure 1). The correlation was less good when more nearly equal divisions such as 0-15 ft, 15-30 ft and over 30 ft were used. They concluded from the graph that the addition of a new layer of foliage of a given volume results in the same increase in BSD no matter which layers are present to begin with. There is no special biological significance attached to the number of layers chosen, and it was suggested that 4 or 5 layers in a similar sort of division would be more accurate. In a later paper, MacArthur (1964) found that the best correlation of BSD to FHD in the tropics is obtained when 4 layers instead of 3 layers are used. From this observation he concluded that the bird community is responding to the
Figure 1 A plot of MacArthur and MacArthur (1961) data showing the relationship of BSD to FHD in eastern U. S. forests. Diversity is measured using the Shannon-Weaver index. FHD is calculated using 3 layers; 0-2, 2-25 and over 25ft.

$R^2 = 0.83$
vegetational structure as if there were 4 distinguishable layers in the tropics and 3 in temperate North America.

The MacArthurs (1961) also indicated that plant species diversity has little effect on bird diversity. However, it did make a difference whether the forest was a mixed hardwood stand or a spruce stand. A spruce forest of similar FHD to a mixed hardwood was found to support greater bird diversity, apparently because conifers have an inside and outside to the canopy. Karr (1968) in his study of bird diversity on strip mined land in Illinois similarly found low correlation between bird diversity and plant species diversity.

Since the MacArthurs' paper there have been a number of additional studies in which FHD and BSD have been measured (MacArthur et al., 1966; Recher, 1969; Karr, 1971). The results of these studies have demonstrated the usefulness of measuring FHD and Recher (1970) concluded that FHD is of proven value and should be included as an important parameter in bird community studies. In each of the studies cited above a major objective was to test the correlation of BSD to FHD and although their results have been in general agreement, the relationship may not hold on recently disturbed areas. Terborgh and Weske (1969) in studying the use of disturbed sites by Peruvian birds present the data plotted in Figure 2. This figure clearly shows no correlation of BSD and FHD in these disturbed habitats. They suggest that the results imply that any disruption of the natural layering of foliage results in a decrease in the total number of species and, conversely that the coexistence of large numbers of
Figure 2 A plot of the data from Terborgh and Weske (1969) illustrating the lack of correlation of BSD to FHD on these disturbed Peruvian sites.
species depends in part on the availability of certain structural relationships that are characteristic of and peculiar to the primary vegetation of the area.

Objectives

The present study developed from the presumption that there is some validity to the diversity-stability dogma and that the bird community contributes significantly to ecosystem function and to the aesthetic value of an area for human visitors. Two related characteristics of the local breeding bird community, the total number of birds present and the diversity of bird species determine the nature and magnitude of its contribution. This study has concentrated on the question of bird species diversity and its relationship to forest structure.

A number of studies done primarily in the eastern United States and western hemisphere tropics have indicated that the pattern of vertical foliage distribution limits breeding bird diversity and provides the framework for the partitioning of bird niches. The objective of this study was to investigate the applicability of this concept to the breeding bird communities of western Montana Douglas-fir (Pseudotsuga menziesii) forests. A series of nine Douglas-fir sites which varied in structural configuration were selected for study. On these sites, breeding bird censuses were made along with measurements of foliage density in horizontal layers from ground level to the

1Vegetation nomenclature follows Hitchcock and Cronquist (1955).
top of the canopy. The foliage density measurements were used to estimate both foliage height diversity, an index of the evenness of the vertical distribution of foliage, and volume of foliage. These values were then tested for their correlation with bird species diversity values calculated from the bird census data.
CHAPTER II

STUDY AREA

Each of the nine sites selected for study is located on or directly adjacent to The Lubrecht Experimental Forest of the University of Montana School of Forestry. Lubrecht is located in the east central portion of the Northern Rocky Mountain Region, about 35 miles east of Missoula in the foothills of the Garnet Range (Figure 3). Figure 4 shows locations of each of the study areas on the Forest.

The forest vegetation of the area is typical of the region. At the lower elevations, ponderosa pine (Pinus ponderosa) is the dominant tree species. With greater moisture available at higher elevations Douglas-fir replaces the ponderosa pine and it is often found in mixed stands with western larch (Larix occidentalis), lodgepole pine (Pinus contorta) or ponderosa pine. Fire and harvesting activity have maintained seral stands of larch and lodgepole pine in association with the Douglas-fir.

Logging began on the forest about 1904 and was completed between 1930 and 1935. Since 1939, when most of the property was deeded to the University by the Anaconda Company, timber harvesting in the immediate study area has been limited to a few experimental cuts and some Christmas tree cutting during the 1950's and 1960's. During the period of active logging most of the forest was high-grade logged
Figure 3  Map showing the location of Missoula in western Montana. Lubrecht Experimental Forest where this study was conducted is located 35 miles east of Missoula.
Figure 4 Location of study areas on Lubrecht Forest
and very little of the area was left uncut.

Much of the land surrounding the experimental forest is managed by the Bureau of Land Management (BLM) and there is considerable logging activity in the Lubrecht vicinity. One of the study sites is located on BLM land. Lubrecht Forest land is leased to local ranchers for grazing, and during the summer months the cattle range over the forest subjecting the more accessible areas to considerable grazing pressure.
CHAPTER III

METHODS

Study Site Selection

A critical phase of this investigation was the selection of a suitable set of study sites. Since the final analysis of the results was necessarily limited by the nature of the set of sites chosen for study, a great deal of time and effort was spent locating and delimiting individual study areas. With the primary objective being to examine the relationship between the foliage profile and bird diversity, a set of study sites was selected that demonstrated a wide range of variation in foliage profile with limited variation in other stand characteristics. Sites were located which formed a series of stands in which Douglas-fir was clearly the dominant tree species with other species only sparsely represented in the overstory and which fit into the sequence of structural configurations illustrated in Figure 5. This sequence of profiles represents a progression from a structurally simple clearcut or meadow to the more complex structure represented by a virgin Douglas-fir stand.

The total number of sites selected was dictated in large part by the number which could be adequately censused by one investigator. Some preliminary observations the preceding summer and Manuwal's (1968) observations on nearby areas of Lubrecht Forest indicated that
Figure 5  Representation of the structural configurations of the forest stands included in this study
the breeding season extends for about 30 days from the end of May to the beginning of July. To insure the reliability of the census data it was felt that each site should be censused at least twice, once early in the breeding period and again later. Taking into account the possibility of bad weather, the number of sites was conservatively limited to nine.

Breeding bird censuses are traditionally conducted over 2 or more acres. Since there can be great structural heterogeneity within 25 acres it seemed inappropriate for this investigation of bird diversity to survey such large areas. MacArthur (1965) suggested that measures of bird diversity should be done over areas large enough to hold 20-25 breeding pairs. Preliminary observations indicated that within the area under study, 7 to 10 acres are required to hold 20 breeding pairs. Limiting the size of the study sites are the additional and critical criteria for this study that (1) all areas be relatively homogeneous vegetationally and (2) that there be a surrounding buffer zone of similar forest structure to minimize the effect of enhanced species diversity at the interface of two forest types.

In spite of the general appearance of homogeneity in the Douglas-fir forest, it proved very difficult to locate large structurally homogeneous forest stands. Topographic diversity and the local history of fire and timber harvest have resulted in considerable patchiness within the forest. Thus, the final process of site selection became one of compromise in locating a set of study areas which illustrated the desired range of structural variation, with each site being large enough to hold an adequate bird population, yet small enough
to be consistent with the requirement of structural homogeneity.

A general description of each of the nine sites is given in Table 1. Sites 1, 3, 4, 9 and 2 represent a sequence of sites whose structural configurations roughly correspond to the illustrations in Figure 5. These 5 are on north-facing slopes, while the additional 4 sites are not limited to northerly aspect and include more variation in structural configuration.

**Bird Census**

An adaptation of the singing male technique originally outlined by Kendeigh (1941) was used in the study. The singing male technique involves slowly traversing the study area on parallel lines close enough together so that every singing male can be heard and located. Each male is identified and his position is noted on a map of the area. After repeated censuses on several mornings, the maps are combined and the territories of each male are identified and areas are calculated. The census is made during the early morning hours shortly after first light when singing activity is most intense and it can be assumed that all the breeding males are present and singing on their territories. Census data obtained in this manner is presumed to include all the breeding males while excluding non-breeders and transients. The validity of the census data depends upon the assumption that the non-breeders and transients do not play a significant role in the ecosystem and can be ignored. Klopfer (1969) indicated that at least during the breeding season this is a valid assumption, and Recher (1970) pointed out that problems associated
<table>
<thead>
<tr>
<th>Site</th>
<th>Aspect</th>
<th>Slope (°)</th>
<th>Elevation (m)</th>
<th>Area (ha)</th>
<th>Structural Configuration</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Stinkwater Clearcut (SC)</td>
<td>N65E</td>
<td>40</td>
<td>1585</td>
<td>8.1</td>
<td>I</td>
<td>Clearcut and slash burned 1962-63. Mostly grassy with very little tree regeneration</td>
</tr>
<tr>
<td>2 Stinkwater Virgin (SV)</td>
<td>N3E</td>
<td>54</td>
<td>1585</td>
<td>2.1</td>
<td>V</td>
<td>Virgin Stand. Largest trees about 240 yrs old</td>
</tr>
<tr>
<td>3 Stinkwater I (SI)</td>
<td>N58E</td>
<td>25</td>
<td>1585</td>
<td>1.8</td>
<td>II</td>
<td>Largest trees about 30 yrs old. Grassy.</td>
</tr>
<tr>
<td>4 Stinkwater II (SII)</td>
<td>N46E</td>
<td>38</td>
<td>1585</td>
<td>1.6</td>
<td>III</td>
<td>Dense stand, largest trees 90-120 yrs old</td>
</tr>
<tr>
<td>5 Section 31 (31)</td>
<td>S5W</td>
<td>56</td>
<td>1650</td>
<td>1.6</td>
<td>IV</td>
<td>Virgin open stand on south aspect. Largest trees 120-200 yrs old.</td>
</tr>
<tr>
<td>6 Mud Creek South (MCS)</td>
<td>S13W</td>
<td>24</td>
<td>1585</td>
<td>2.7</td>
<td>IV</td>
<td>Open stand, grassy with clumps of saplings. Largest trees 140-90 yrs old.</td>
</tr>
<tr>
<td>7 BLM (BLM)</td>
<td>N28E</td>
<td>40</td>
<td>1650</td>
<td>1.6</td>
<td></td>
<td>Harvested by overstory removal about 15 yrs prior to study, very thick shrub layer.</td>
</tr>
<tr>
<td>8 Stinkwater West (SW)</td>
<td>S62W</td>
<td>39</td>
<td>1620</td>
<td>2.0</td>
<td>IV</td>
<td>Open stand, very sparse undergrowth. Largest trees 140-190 yrs old.</td>
</tr>
<tr>
<td>9 Mud Creek North (MCN)</td>
<td>N42W</td>
<td>23</td>
<td>1585</td>
<td>2.6</td>
<td>V</td>
<td>Many very large stumps. Thick undergrowth. Largest trees 130-200 yrs old.</td>
</tr>
</tbody>
</table>

1See Figure 5 for description.
with making an accurate census which includes non-breeders and transients make it very difficult to test the assumption.

The censuses for this study were done by walking slowly around the boundary of the sites in the early morning. The presence of each male heard within the boundaries was noted and his approximate position was plotted on a sketch map of the area. After walking around the area once, time was spent within the site to verify the presence of birds initially counted and to reduce the possibility of missing any of the breeding males. Each of the 9 study areas was censused in this manner at least twice during the breeding period from June 3 to July 1, 1973.

Because of the limited number of counts for each site and the small size of the study areas, it did not seem practical to attempt to delimit territorial boundaries. Instead a singing male's position was noted on a sketch map of the area only to identify it as being inside or outside the boundary. A bird was given full status as a resident if it was heard and seen within the boundary, even if its territory may have actually extended off the area. Similarly, birds which were singing just off the area were not included even though their territories may have extended into the study area. Because of the technique, some differences were noted between censuses of the same area on different days. Some of the discrepancies were resolved by supplemental observations at other times of the day such as finding a nest or observing adults carrying food. A few discrepancies were resolved by arbitrarily selecting the census information in which I had the greatest confidence. For example, Chipping Sparrows and
Juncos sang very early and then quieted down as the census continued, so in the case of these species, a census done earliest in the morning was given more weight. Cloudy or unusually cold mornings also changed the singing activities of the birds so that censuses on such days were given less weight. Birds which were obviously just passing through, such as Pine Siskins or Evening Grosbeaks were not included in the census nor were birds which were heard singing once or twice within the area and then moved elsewhere. Nuthatches and woodpeckers were observed in this latter category on almost all of the study areas but never were included in any of the censuses.

**Vegetation Measurement**

After the sites had been located and the boundaries had been marked, each area was surveyed using staff compass, abney level and chain. Maps were drawn and the area covered by each site calculated from the map. Within each site 25 x 25m grid points oriented along the long axis of the study area were marked out. Using the grid, a procedure was developed to randomly locate sample points. A table of random numbers was used to (1) select a grid point (2) a direction and distance to be measured parallel to the long axis and (3) a direction and distance to be measured perpendicularly to the long axis. This procedure determined the position of the center of a sample plot of eight meters radius, within which measurements of the vegetation were

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1Avian nomenclature throughout follows the American Ornithologist's Union Checklist (1957, 1973).
made. Eight such sample plots were located on each study site. Overlap between sample plots was not allowed, nor were sample plots established that extended outside the boundary of the study site.

The major measurement made on each sample plot was that of foliage densities. Most other studies of this kind have measured foliage density following a procedure developed by MacArthur and MacArthur (1961). Their method involved measuring the horizontal distance a plate must be moved from an observer before half of its area is obscured by foliage. An estimate of the foliage density can be obtained from the equation \( K = \ln \frac{2}{D} \), where \( D \) is the distance from the plate to the observer and \( K \) is the foliage density. Measurements are made at various levels and from this a foliage profile can be constructed. A number of practical problems involved in making these sorts of measurements in tall forest stands led to the conclusion that this method was inappropriate for this study. Orians (1969) employed a technique suggested by MacArthur and Horn (1969) involving placing a camera with a telephoto lens on a tripod over a randomly selected point and aiming it upwards. By adjusting the focus, the distance to the first leaf can be measured. Combining these readings with other measures made of the proportion of the sky not obscured by foliage, MacArthur and Horn present a theory which makes it possible to calculate foliage densities at various levels. This technique suggested the method actually used in this study.

A pole marked off in 0.2m segments was constructed which could be extended vertically over a sample point to a height of 15m. The estimated proportion of each 0.2m segment touched by foliage was used
as the estimate of foliage density. Over some points the pole could not be extended the full 15m and at other points, foliage extended above 15m. In these cases a direct measurement was not possible and the foliage density had to be estimated at higher levels by a less precise method. Based on direct measurements made at the lower levels a reference value for moderately dense foliage was established. Then by visually comparing the foliage density over the point being measured with the reference value, a foliage density value was assigned to that portion of the canopy beyond the reach of the pole. The height of the canopy was measured by means of a clinometer and the foliage was assumed to be evenly distributed over this distance and the estimated foliage density value was assigned to each meter of foliage above the pole.

At each sample plot center, an azimuth was selected from random number tables, an eight meter transect was laid out in that direction, and the foliage density measurements were made at one meter intervals along that transect. A summation of the eight measurements made along the transect was used to develop the foliage profile for the sample plot. Since eight sample plots were used on each study area, the foliage profiles for each site were based on a summation of data from the eight sample plots within the area. An index of the total foliage volume for a study site was taken as a summation of all the foliage density measurements over each of the 64 transect points.

**Diversity Calculation**

In other investigations of bird diversity, two different
diversity indices have been used; \( H' = -\sum P_i \ln P_i \) and \( D = \frac{1}{\sum P_i^2} \). The former is the Shannon-Weaver index which has been adapted from information theory and has been used extensively in ecological diversity studies. The latter is one suggested by MacArthur and Wilson (1968) and MacArthur (1972). Of the two, \( H' \) has been most widely used in a variety of studies involving birds and other groups of organisms.

In the application of either of the two indices to the bird census, \( P_i \) is taken as the proportion of individuals in the \( i \)th species. For use in describing the foliage profile, \( P_i \) is the proportion of the foliage in the \( i \)th layer.

On the basis of MacArthur's (1972) suggestion that \( D = \frac{1}{\sum P_i^2} \) is a useful measure of diversity in competitive communities and because it more directly reflects the number of equally represented categories, it was chosen as the measure of diversity in this study. In addition, this index showed a much clearer relationship of FHD and BSD than did \( H' \). Also as pointed out by MacArthur, it has the subsidiary attribute of being easily calculated on desk calculators.
CHAPTER IV

RESULTS AND DISCUSSION

Bird Census

The results of the bird censuses are presented in Table 2. This table lists the species encountered and the number of singing males on each of the study sites. On the nine sites a total of 21 species and 132 singing males were counted.

Foliage Density and Foliage Height Diversity

The foliage density data is presented as foliage profile diagrams for each of the nine study areas in Figure 6. These profiles illustrate the vertical distribution of the foliage with the horizontal axis representing a relative density value.

Four different FHD values were calculated using four different patterns of dividing the foliage into layers (Figure 7). FHD 1 was calculated using 3 layers; 0 - 1.0m, 1.0 - 8.0m and over 8m. For FHD 2, the foliage was divided into 1.0m layers with the number of layers being determined by the height of the foliage profile. Division of the foliage for the calculation of FHD 3 is similar to FHD 2 except that only the first 12 meters of the foliage profile was included, and FHD 4 was calculated based on a division of the first 15 meters into
<table>
<thead>
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<th>SC</th>
<th>SV</th>
<th>SI</th>
<th>SII</th>
<th>MCS</th>
<th>BLM</th>
<th>SW</th>
<th>MCN</th>
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<td>1</td>
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<tr>
<td>Dusky Flycatcher</td>
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<td></td>
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<tr>
<td>Mountain Chickadee</td>
<td>1</td>
<td>1</td>
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<td></td>
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<td>Brown Creeper</td>
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<tr>
<td>Robin</td>
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<td>Hermit Thrush</td>
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<td>Swainson's Thrush</td>
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<td>Golden-crowned Kinglet</td>
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<td>13</td>
<td>14</td>
<td>17</td>
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( # singing males)
Figure 6. Foliage profiles of the nine study sites.
Figure 6. (continued)
Figure 7  Illustration of the manner in which the foliage profiles were partitioned into layers for the calculation of the 4 FHD values.
<table>
<thead>
<tr>
<th>Site</th>
<th>BSD</th>
<th>FHD 1</th>
<th>FHD 2</th>
<th>FHD 3</th>
<th>FHD 4</th>
<th>Volume Index</th>
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<td>SC</td>
<td>3.189</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>34.0</td>
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<td>4.235</td>
<td>1.885</td>
<td>11.186</td>
<td>2.496</td>
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<td>186.0</td>
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<td>7.654</td>
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<td>31</td>
<td>5.444</td>
<td>2.194</td>
<td>11.588</td>
<td>5.705</td>
<td>9.510</td>
<td>130.4</td>
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<tr>
<td>SW</td>
<td>7.000</td>
<td>2.134</td>
<td>11.635</td>
<td>5.947</td>
<td>9.311</td>
<td>107.7</td>
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</table>
lm layers and division of the upper canopy into 5m layers. These four FHD indices as well as the index of foliage volume and BSD values for each site are presented in Table 3. The rationale for the use of these four FHD indices in the analysis of the foliage profiles will be developed more completely in the discussion of the relationship of BSD to FHD.

Bird Diversity and Foliage Height Diversity

The results of the present study indicate that the bird community does respond to the evenness of foliage distribution, but not in the layers suggested by MacArthur. There is also an indication that, contrary to the study of Terborgh and Weske (1969) disturbed sites have higher BSD than might otherwise be predicted in terms of FHD.

An examination of Figures 8 - 11 provides an insight into the manner in which the bird community is responding to the foliage profile. In Figure 8, the foliage has been divided into three layers; 0 - 1.0m, 1.0 - 8.0m and 8.0m for the calculation of FHD 1. This division corresponds closely to the layers chosen by MacArthur and MacArthur (1961). A plot of the BSD values against FHD 1 in Figure 8 suggests a trend of increasing BSD with increasing FHD 1 although the correlation is weak as reflected by the r^2 value of 0.34. This figure compares with the MacArthur's (1961) data plotted in Figure 1, where the correlation was positive and strong (r^2 = 0.83). While the foliage densities were not measured in the same manner, the implication from a comparison of these two figures is that the bird com-
munity in these Douglas-fir stands is not responding to the foliage profile in the same manner as the eastern birds in the MacArthur's study.

In Figure 9, BSD is plotted against FHD 2. This calculation of FHD, based on division of the foliage into 1m layers, shows a greater correlation ($r^2 = 0.51$) than noted in Figure 8. An impression gained during the process of censusing and walking in the forest was that the birds were more abundant and more species were present where there was a well-developed brush layer. This observation suggested that the upper layers of canopy might be less important and prompted the calculation of FHD 3 where only the first 12m of the foliage profile was included. The first twelve meters also represent the limit of greatest accuracy in measuring foliage densities. BSD is plotted against FHD 3 in Figure 10. This treatment only slightly changes the correlation; $r^2 = 0.55$ compared with 0.51 in Figure 9, but suggests that the addition of equally represented foliage layers up to 12m is of greater importance in making room for additional species than the addition of foliage above 12m. Based on this observation, FHD 4 was calculated, where 1m increments were used up to 15m and 5m increments from there up. This has the effect of reducing the FHD 2 values of the sites with the tallest trees, and does not change the values for the sites with no foliage above 15m. A plot of BSD against FHD 4 in Figure 11 shows an improvement in the correlation ($r^2 = 0.71$). There is also the suggestion in Figure 11 that something is unusual about the site labelled BLM. It has an unusually high BSD and predicted by FHD 4 when compared with the other sites. BLM is a disturbed site
Figures 8 - 11 BSD values are plotted against the four FHD values.
Figure 10

$\tau^2 = 0.55$

Figure 11

$\tau^2 = 0.71$
having been recently harvested by an overstory removal. There are scattered Douglas-fir trees and a well established brush layer of huckleberry (Vaccinium spp.) and snowberry (Symphoricarpos albus).

**Bird Species Diversity and Foliage Volume**

It seems reasonable to expect that the total volume of foliage might be important to the bird community. However, when the index of foliage volume is plotted with BSD, there is no obvious relationship (Figure 12). When a linear model is used, the $r^2$ value is 0.28 and a quadratic model shows even less correlation with an $r^2$ of 0.16. A multiple regression of BSD on FHD 4 and volume resulted in a lower $r^2$ value from that obtained when FHD 4 was used alone. A linear regression of FHD 4 on volume has an $r^2$ value of 0.59. These results suggest that while FHD 4 is at least in part determined by the total volume foliage, the bird community is more directly responding to the evenness of foliage distribution than to the volume of foliage.

**Foraging Niche Diversity**

A bird species list and the diversity value based on the species count provides only a limited description of the diversity present in the bird community. A more complete description of the diversity should reflect the distribution of species by trophic levels and the range of foraging behaviors exhibited by the species present in the community. In an effort to develop this kind of description of the bird communities, the foraging behaviors of each species encount-
Figure 12 BSD is plotted against the index of foliage volume illustrating the lack of correlation between BSD and foliage volume.
Seven different foraging behaviors were recognized for the species included in the censuses; ground gleaning-seeds (GGS), ground-brush gleaning (GBG), hawking (H), bark gleaning (BG), Flycatching (FC), foliage gleaning-creeping (FGC) and foliage gleaning-hovering (FGH). A description of each of these foraging behaviors is given in Table 4. The species accounts in Bent's life histories (1912, 1916, 1918, 1919, 1950, 1953, and 1958) supplemented by Manuwal (1968) and personal observations were used to characterize the foraging behaviors of the species encountered (Table 5). Note that many of the species exhibit more than one foraging behavior. No attempt was made to identify the most favored foraging technique and, unless a behavior was noted as being uncommon, each behavior reported or observed was assigned to that species.

In Table 6, the information from Table 5 is applied to the species lists for each of the study areas. The number in the far right-hand column headed Foraging Niche Diversity (FND) is the total number of entries for each study area. FND is being used here to reflect the total range of foraging behaviors exhibited by the bird community. A plot of FND against FHD 4 in Figure 13 shows a good correlation of FND and FHD 4 ($r^2 = 0.73$). Of particular interest is the fact that, when the data is treated in this manner, the ELM site does not appear to have unusually high diversity. In terms of species diversity BLM is more diverse than would be predicted by FHD 4, but when the range of foraging behaviors is considered it does not appear to be unusually diverse.
<table>
<thead>
<tr>
<th>Foraging Behavior</th>
<th>Description</th>
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<tbody>
<tr>
<td>Ground gleaning-seeds GGS</td>
<td>Scratching in litter to feed on seeds.</td>
</tr>
<tr>
<td>Ground-brush gleaning GBG</td>
<td>Foraging on ground and in low shrubs for insects.</td>
</tr>
<tr>
<td>Hawking H</td>
<td>Jumping from low perch to pick up prey on ground.</td>
</tr>
<tr>
<td>Bark gleaning BG</td>
<td>Moving up and down bole, gleaning prey from bark.</td>
</tr>
<tr>
<td>Flycatching FC</td>
<td>Catching prey aerially; usually involves sitting on perch then darting out when prey is sighted</td>
</tr>
<tr>
<td>Foliage gleaning-creeping FGC</td>
<td>Moving around on foliage searching for prey</td>
</tr>
<tr>
<td>Foliage gleaning-hovering FGH</td>
<td>Hovering while picking prey from foliage</td>
</tr>
<tr>
<td>Species</td>
<td>Symbol</td>
</tr>
<tr>
<td>-------------------------</td>
<td>--------</td>
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<tr>
<td>Dusky Flycatcher</td>
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</table>

FORAGING BEHAVIORS OF SPECIES
ON EACH STUDY SITE
(See Table 5 for explanation of species symbols)
Figure 13 Foraging niche diversity is plotted against FHD 4.
CHAPTER V

CONCLUSION

The number of bird species which can coexist in a particular environment is limited by the number of bird niches which can be partitioned within the environmental hypervolume. A strict interpretation of Hutchinson's (1957) concept of the niche involves a multidimensional analysis of the niche space occupied by the species and suggests that the environmental hypervolume is partitioned along many resource continua. In practice however, such a multidimensional analysis is not possible; and, when considering a single group of related species in a competitive community, it is generally possible to identify one or a few resource continua along which competition is most intense and which appear to be most important in partitioning the environment into niches (Levins, 1968).

For a bird community, two reasonable continua to consider are food types and size classes and as suggested by MacArthur (1958) for wood warblers, positions in the canopy in which to forage for insects. MacArthur and MacArthur (1961) later extended this to suggest that the bird community is partitioning the environment on the basis of the foliage profile. A number of later studies, this one in the Northern Rockies included, have shown that there is indeed a strong relationship between bird species diversity and the foliage profile.
when the profile is described in terms of foliage height diversity.

This relationship indicates that while the food resource is probably the most important limiting resource, it may be indirectly partitioned by way of foraging niches which are partitioned on the vegetational substrate. Investigations of food preferences of bird species indicate that while each species may take food types and size classes in different proportions, there is considerable overlap among species (e.g. Wiens, 1973). Additionally, many bird species are opportunistic, readily switching to prey which are present in large numbers, such as spruce budworm during an outbreak. On the other hand, careful examination of foraging behaviors demonstrate that bird species take prey in different manners (MacArthur, 1958); so while several species may be feeding on the same prey population, they are each exposed to a different portion of the population. The correlations of both bird species diversity ($r^2 = 0.71$) and foraging niche diversity ($r^2 = 0.73$) with foliage height diversity suggest that the foliage profile is a good indicator of the potential for differentiation of the environment into bird niches.

Examination of the correlation of bird species diversity with the four foliage height diversity indices in this study suggest that the bird community in these Northern Rocky Mountain Douglas-fir stands is responding to the foliage profile as if it were made up of many layers, contrary to the findings of MacArthur (1964) where he concluded that the bird community was responding to the vegetational structure as if there were 3 layers in temperate forests and 4 layers in tropical forests. It also appears that the lower 12 - 15m of the foliage pro-
file are of greatest importance in regulating bird diversity. The correlations of bird species diversity with a foliage height diversity index based on the entire foliage profile and another index developed using only the first 12m are not substantially different ($r^2 = 0.51$ and 0.55). The canopy above 12m does contribute to the prediction of bird diversity, but it is as if it requires a thicker layer of upper canopy to be equivalent to a lower layer in increasing the potential for niche differentiation. When foliage height diversity is calculated by dividing the foliage profile into 5% layers above 15m and 1m layers below 15m, the best correlation of bird species diversity to foliage height diversity is obtained ($r^2 = 0.71$).

These observations suggest that the environment occupied by the forest bird community can be thought of as a volume being built up of layers of vegetation. The first layer is made up of grasses and herbs, on top of which may be added a number of shrub layers and finally the layers which constitute the canopy, with a thicker layer of canopy being required to equal a lower layer. A single layer of vegetation may satisfy the requirements of several species; because of the limited range of foraging possibilities within that one layer, interspecific competition would limit the number of species which can be accommodated. Addition of another layer of vegetation can result in the addition of new species because the range of movement has been increased and thus provided an avenue to reduce interspecific competition.

The linearity of the relationships of bird species diversity and foraging niche diversity with foliage height diversity suggest
that the addition of new layers of foliage results in a proportional increase in foraging niches and bird species diversity. As the additional layers are being added two things are happening which help to account for increased bird diversity. With the increase in the number of equally represented layers, the food resource is becoming more widely distributed thus increasing the possibilities for partitioning the food resource. Also since the total vegetational substrate will generally increase with more foliage layers, it seems reasonable to expect that the insect food resource should also be increasing in response to a greater substrate.

The above analysis suggests that both the evenness of the foliage profile and the volume of vegetation should be important in regulating bird diversity. If the total volume of vegetation is low, even if it is evenly distributed, the food resource will be limited and relatively few bird species and a small overall bird population can be supported. On the other hand, it might be expected that as the total environmental volume begins to fill up with foliage some potential niches might be eliminated. Flycatching, for instance, would be reduced as a foraging activity. There is thus some theoretical reason to expect that a curvilinear model for the relationship of bird species diversity to foliage volume (Figure 14) might be valid, though the limited number of data points do not adequately support the model.

The foregoing discussion applies only to a structurally homogeneous area. Horizontal heterogeneity and the presence of special features such as rock outcrops and watercourses would enhance the
Figure 14  A quadratic model for the relationship of BSD to foliage volume drawn on the plot of BSD and foliage volume.
possibilities for niche differentiation within a given area. Furthermore, although the foliage profile may be used to predict the diversity of bird species, it has limited value for predicting which species will be present. MacArthur et al (1962) found this to be the case when they tried to use the foliage profile to make predictions about the bird census. Presence or absence of particular species is probably more directly related to the presence or absence of special habitat requirements such as nest sites than to foliage profile.

A final result of this study indicates that expected bird diversity and thus niche relationships may be altered on recently disturbed sites. A site which had been harvested by an overstory removal showed enhanced bird diversity over that which would be predicted by regression of bird species diversity on foliage height diversity, although the diversity of the bird community measured by foraging niche diversity did not appear unusually high. The other severely disturbed site, a clearcut, did not show the same enhancement in diversity. The possible enhancement of diversity on recently harvested forest sites is deserving of note and it is important that this phenomena be further studied on a variety of forest sites.


