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Seasonal Variations in Forest Birds of Western Oregon

Introduction

The western part of Willamette Valley, Oregon grades from an open savannah-like area into dense Oregon white oak (*Quercus garryana*) woods which probably originally developed there following settlement by white man, who prevented the brush fires which previously maintained the oaks in an open savannah. The increased shade from dense canopy in such woods prevents oak seedlings from growing, allowing Douglas-fir (*Pseudotsuga menziesii*) to germinate under the oak canopy in dry areas. In moist areas near streams, washes, and north-facing slopes, big leaf maple (*Acer macrophyllum*) develops, and grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), or western red cedar (*Thuja plicata*) follow Douglas-fir in succession depending on altitude and exposure.

Within the three major vegetative types oak-fir-hemlock, I sought to characterize the seasonal changes in bird species composition, diversity, and ecological structure. Ten study areas were used. A permanent transect was established with a surveyor's tape in each area so that the same portion could be censused for avifauna composition on each visit. The areas varied from a pure oak stand through the Douglas-fir sere into the western hemlock sere.

Methods

To record and compare the avifaunal composition of several sample plots, a method was sought which would give a relative abundance index rather than an absolute population count. Four methods were selected for analysis: the strip census, the strip map, the point quarter, and the sample count. Each method was used in the same 120-acre stand of Oregon white oak located on the north-facing slope of Pigeon Butte, 12 mi south of Corvallis, Oregon (T13S, R5W, Sec. 31, N.E.-¼) in the spring of 1967.

Care was taken to conduct all censuses under similar conditions. Thus, all censuses were made between 0600 and 0900 on sunny, calm mornings. The results of censusing which began on May 15 and continued through June 4 were recorded in Table 1. Periodic censuses were made during the fall and winter. The following spring, the procedure was repeated in several conifer stands to see if the method selected could be used in all stands on an annual basis.

All birds seen in the vegetation were counted. When a singing bird was heard, an attempt was made to see if it was within the census area. If so, it was counted only if visually observed. When a presumed singing male was found, an attempt was made to locate the female. The female was not counted unless she was observed within the census area.

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TABLE 1. Comparison of four census methods.

Species	Census Method[1] Strip Census	Strip Map	Point Quarter	Sample Count
Ring-necked Pheasant	1.6	0.0	0.0	0.0
Hairy Woodpecker	3.1	2.2	2.9	0.0
Downy Woodpecker	3.1	2.2	2.9	2.0
Western Wood Pewee	0.0	0.0	0.0	3.9
Black-capped Chickadee	4.7	8.9	5.9	7.8
Common Bushtit	6.3	6.7	5.9	5.9
White-breasted Nuthatch	3.1	4.4	5.9	3.9
Red-breasted Nuthatch	3.1	2.2	2.9	2.0
Brown Creeper	1.6	2.2	2.9	3.9
Bewick's Wren	0.0	4.4	2.9	3.9
Robin	9.4	4.4	5.9	5.9
Hutton's Vireo	0.0	2.2	2.9	2.0
Solitary Vireo	6.3	4.4	2.9	3.9
Warbling Vireo	3.1	2.2	2.9	3.9
Orange-crowned Warbler	12.5	11.1	8.8	7.8
Yellow Warbler	0.0	0.0	2.9	2.0
Audubon's Warbler	1.6	0.0	2.9	2.0
MacGillivray's Warbler	3.1	8.9	2.9	3.9
Wilson's Warbler	9.4	6.7	5.9	5.9
Western Tanager	3.1	4.4	2.9	3.9
House Finch	6.3	4.4	5.9	3.9
Rufous-sided Towhee	9.4	8.9	8.8	9.8
Oregon Junco	3.1	4.4	5.9	3.9
Chipping Sparrow	6.3	4.4	5.9	7.8
Species recorded	20	20	22	22

[1] Relative density of species.

The Strip Census Method. Using the strip census methods of Forbes and Gross (1923), five 120-ft wide strips were located parallel to one another, 500 ft apart. Each strip was 1000 ft long. The width of these strips was established on the basis of preliminary observations which indicated that I could see and flush birds up to 60 ft on each side of the strip. Beyond that distance, differences in the conspicuousness of individuals and species provided a source of bias. To census an area, I walked slowly along the center of the strip counting all birds seen within the 60 ft on either side.

The Strip Map Method. The second method used was an adaptation of the strip census method using a map of the region. A single transect 120 ft wide and 3000 ft long was established. This transect crossed the five strips used in the strip census method at right angles. Important topographic and vegetative features were marked on the map, which was duplicated and used to record the location of all birds seen as I walked down the center of the mapped rectangle.

The Point Quarter Method. Using this method, which was originally proposed for phytosociological sampling by Cottam and Curtis (1956), 10 points were selected by means of a random numbers table along the same 3000-ft transect used in the strip map method. The space around each point was divided into four quarters by bisecting the transect at a 90° angle. As I could observe birds for a distance of 60 ft in all directions, each quarter consisted of one-fourth of a circle with a 60-ft radius. When I reached a point, the first bird seen in a tree, on a shrub, and on the ground in each quarter was recorded; sometimes no bird was seen in one or more of these positions. Birds heard were not recorded unless they moved into view.

The Sample Count Method. This method was first used for bird population studies by Bond (1957). In my study, I established 10 observation points at intervals of 312 ft along a transect through the stand. As I walked through the stand, I stopped at each sample point for 10 minutes and recorded all birds seen within 60 ft of the point. Following the 10-minute stop, I walked slowly to the next point, recording all birds seen within 60 ft on either side of the transect.

In Table 1, the relative density for each species was calculated by dividing the number of individuals of that species by the total number of individuals seen. Three censuses were made of the stand with each of the methods, and the largest number of individuals per species recorded during these three times was considered as the local population of the species. As this was the breeding season, nomadic wandering of groups of birds was at a minimum.

The minimum time required for each method was as follows: strip census—three hours; strip map—two and a half hours; point quarter—two and a quarter hours; sample count—three hours.

The largest number of individuals was observed when the sample count method was used. This was probably an outcome of the 10-minute waiting period made at each stop. Some species were inevitably disturbed when an observer moved through heavy understory. Some birds such as the warblers, vireos, and chickadees may stop their activity or leave the area. Other species like the Rufous-sided Towhee (*Pipilo erythrophthalmus*) may be flushed by the approaching observer. In general, the different methods recorded similar numbers of species, although the sample count and quarter methods listed two more species than the strip map and strip census methods.

Twenty-one species were recorded in common by the sample count and quarter methods. This was the largest number of species shared by any two methods. The largest number of individuals was observed using the sample count method and the fewest with the quarter. Both methods thus appeared equally sensitive to the species composition of the stand, although the quarter method, because it recorded only the first bird seen in a particular stratum, underestimated the density of individuals in strata of great concentration and overestimated the population in strata of smaller concentrations of birds. The quarter method was founded on the assumption of random distribution of individuals in the community sampled (Cottam and Curtis, 1956). Birds are known not to be randomly distributed because of behavioral and environmental interactions. When one confines his study to a limited area such as an oak stand, a random census method such as the quarter method therefore would be expected to give an inaccurate representation of the avifaunal composition; that the method measured the species composition so well was surprising.

While using the strip census method, it was felt that many birds were being counted more than once as they flew across the strips and the observer walked back and forth. Utilizing the strip map, quarter, and sample count methods, it was felt that this duplicate counting was reduced. It was often possible to keep track of the birds as one moved along the transect. This, however, was not accurate and duplicate counting remained a problem with all of the methods.

Both the sample count and the quarter methods indicated the largest number of species present; however, the sample count showed a considerably larger total number of birds present. Time-wise, the sample count took a little longer; however, the total picture of the avian population appeared more accurate. Thus, the sample count method was adopted for this study. Continued analysis of the sample count method yielded similar results in all forest types throughout the year.

The Study Areas

The 10 study areas used in this study were located on the eastern slope of the coast range (Table 2). A permanent transect was established in each area and censuses were conducted at least once a month between January 1968 and January 1970. All morning censuses were begun one hour after sunrise. Evening censuses were made once each season beginning one hour prior to sunset. During the breeding season (April to August), avian population fluctuated greatly so weekly censuses were made in each study area.

The study sites were divided into the three vegetative types as follows: areas one and two, Oregon white oak with a dense understory of poison oak (*Rhus diversiloba*); areas three through eight, Douglas-fir with Oregon grape (*Berberis aquifolium*), bracken fern (*Pteridium aquilinum*), and many other shrubs.

Results

Typically, avifaunal activity followed different seasons than the four-season calendar. Food supply, nesting material, climate, cover sites, and other factors contributed to changing avifaunal composition and activity. Twomey (1954), in a study of the elm-maple forests in central Illinois, recognized six avifaunal seasons. Anderson (1970) found that the birds of Oregon white oak habitats followed a seasonal pattern similar to the birds of the elm-maple community. They were:

Winter	November 2 through March 1
Early Spring	March 2 through April 15
Late Spring	April 16 through June 1
Early Summer	June 2 through July 15
Late Summer	July 16 through September 1
Fall	September 2 through November 1

The birds of the Douglas-fir and western hemlock communities followed the same seasonal patterns as did the birds in Oregon white oak stands. This study, therefore, was conducted within the framework of these six seasons (Tables 3, 4 and 5).

Bird species were classified as permanent residents, summer residents, winter resi-

TABLE 2. Features of the study areas.

Area Number	Size in Acres	Location	Exposure	Trees per Acre	Height Class Distribution <30′	30-60′	>60′	Percent Canopy Cover
1	120	T13S, R5W, Sec. 31, NE¼	N	110	16	39	45	82
2	125	T10S, R5W, Sec. 27, SE¼	E	117	42	37	20	72
3	105	T11S, R5W, Sec. 9, NW¼	E	90		15	85	61
4	200	T11S, R5W, Sec. 7, SW¼	N	115	3	9	88	86
5	140	T11S, R5W, Sec. 8, SW¼	W	60	5	10	85	89
6	90	T12S, R7W, Sec. 15, NW¼	S	172	2	4	94	98
7	125	T12S, R7W, Sec. 10, SE¼	E	65		7	93	64
8	140	T11S, R5W, Sec. 8, SE¼	N	54		10	90	89
9	110	T12S, R7W, Sec. 16, NW¼	N	152	2	8	90	72
10	115	T12S, R7W, Sec. 9, SE¼	W	164	4	8	88	78

dents, and occasional visitors, based on the time spent in the community and the type of occupancy. Some species were classified differently in different communities. Permanent residents were observed during all seasons and were either directly observed nesting or presumed to be nesting on the basis of indirect evidence (*e.g.*, territorial

TABLE 3. Population census results for avifauna of Oregon white oak.[1]

		Season					
Species	(Resident Type)[2]	Winter	Early Spring	Late Spring	Early Summer	Late Summer	Fall
Turkey Vulture	(O)		22	11	33	22	22
Red-tailed Hawk	(O)	11	22	11	11	11	11
Ring-necked Pheasant	(O)	22	11				
Band-tailed Pigeon	(O)				66	22	55
Great Horned Owl	(O)			1			
Rufous Hummingbird	(S)				11		
Red-shafted Flicker	(O)		44		22		
Pileated Woodpecker	(O)				2		
Yellow-bellied Sapsucker	(O)	11					
Hairy Woodpecker	(P)	11	22	22	11	11	11
Downy Woodpecker	(P)	11	22	22	22	11	11
Western Wood Pewee	(S)		11	22	22	22	22
Steller's Jay	(W)	33					
Scrub Jay	(P)			11			
Crow	(O)		11				
Black-capped Chickadee	(P)	132	110	110	110	154	198
Common Bushtit	(P)	33	22	44	44	22	33
White-breasted Nuthatch	(P)	44	66	44	88	88	44
Red-breasted Nuthatch	(W)	22					
Brown Creeper	(P)	44	66	44	66	66	22
Winter Wren	(W)	11	11				
Bewick's Wren	(P)	11		22	22	11	
Robin	(P)	22	22	88	66	11	11
Varied Thrush	(W)	33	33				
Hermit Thrush	(S)			11	22		
Western Bluebird	(O)	33					
Townsend's Solitaire	(O)		11				
Golden-crowned Kinglet	(W)	22	77				66
Ruby-crowned Kinglet	(W)	33					
Cedar Waxwing	(O)	33					
Hutton's Vireo	(P)	11	22	22	22		11
Solitary Vireo	(S)			22	33		
Warbling Vireo	(S)			22	22		
Orange-crowned Warbler	(S)			66			
Yellow Warbler	(S)			22	22		
Audubon's Warbler	(O)	11					
Black-throated Gray Warbler	(S)			22	22		22
Townsend's Warbler	(S)		22	22	22		
MacGillivray's Warbler	(S)			44	44		
Wilson's Warbler	(S)			44			
Brown-headed Cowbird	(S)			11	22		
Western Tanager	(S)			44	66		
House Finch	(S)			44	44		
American Goldfinch	(S)				66		
Rufous-sided Towhee	(P)	55	44	88	88	44	44
Oregon Junco	(P)	88	44	66	66	33	33
Chipping Sparrow	(S)			44	44		
Golden-crowned Sparrow	(O)			66			
Total species		23	21	30	30	14	16

[1] Converted to birds per 100 acres.
[2] P=permanent resident.
S=summer resident.
W=winter resident.
O=occasional resident.

occupancy). Summer residents included species which arrived in early or late spring, nested, and then left during the spring or summer periods. Occasional visitors were birds that moved through the area, foraged for a short period of time, and then left. This category included birds that visited the area during migration.

During the winter, most of the bird species formed flocks. Single-species flocks of Oregon Juncos (*Junco oreganus*), Ruby-crowned (*Regulus calendula*) or Golden-crowned Kinglets (*Regulus satrapa*), or Common Bushtits (*Psaltriparus minimus*) were common. Mixed-species flocks generally included chickadees, nuthatches, creepers, and woodpeckers. The above flocks were the most common groupings of birds observed during winter. Birds found in the oaks during the winter consisted of permanent residents and a few winter residents such as Winter Wrens (*Troglodytes troglodytes*) and Varied Thrushes (*Ixoreus naevius*). Permanent residents of the higher-elevation coniferous stands which expanded their habitat occupancy became winter residents in oak stands. The fir and hemlock areas had no winter residents as such. All bird species recorded in these areas during the winter were permanent residents.

TABLE 4. Population census results for avifauna of Douglas-fir.

Species	(Resident Type)[1]	Winter	Early Spring	Season Late Spring	Early Summer	Late Summer	Fall
Turkey Vulture	(O)			11	11	5	
Red-tailed Hawk	(O)			1		1	
Blue Grouse	(P)		22				
Ruffed Grouse	(P)		22				
Great Horned Owl	(O)		1	1			
Rufous Hummingbird	(S)				22		
Hairy Woodpecker	(P)			22	22		
Downy Woodpecker	(P)			22			
Western Wood Pewee	(S)				44		
Steller's Jay	(P)			22	44	22	
Chestnut-backed Chickadee	(P)	176	198	154	66	176	132
Red-breasted Nuthatch	(P)	44	44	66	44	99	88
Brown Creeper	(P)	22	44	44	55	44	44
House Wren	(S)			22	44	44	
Winter Wren	(P)	22	22	44		22	22
Golden-crowned Kinglet	(P)	88			22		
Hutton's Vireo	(S)			22	22		
Solitary Vireo	(S)			22			
Orange-crowned Warbler	(S)			22			
Audubon's Warbler	(S)			22			
Townsend's Warbler	(S)			22			
Hermit Warbler	(S)			44	44	22	
MacGillivray's Warbler	(S)			22	22	22	
Wilson's Warbler	(S)			22	22		
Western Tanager	(S)			44	44		
Black-headed Grosbeak	(S)				22		
Purple Finch	(S)			22			
House Finch	(S)			11			
Pine Siskin	(S)		22				
Red Crossbill	(P)					44	
Rufous-sided Towhee	(P)			22			
Oregon Junco	(P)	22	22	66	44	66	110
Total species		6	9	24	17	12	5

[1]P=permanent resident.
S=summer resident.
W=winter resident.
O=occasional resident.

Altitude as well as the presence or absence of foliage may play a role in the type of wintering species found in the areas. When the total number of individuals present during each of the seasons in the study areas was calculated as a percentage of the total for the season having the largest number of individuals, the values in oak stands were somewhat higher than those for coniferous areas (Table 6). An influx of winter residents was largely responsible for this difference. Only 69 percent of the individuals wintering in oaks were permanent residents, while 100 percent of the birds in conifers were permanent residents (Fig. 1).

During early spring, permanent residents in the study areas began to establish

TABLE 5. Population census results for avifauna of western hemlock.

Species	(Resident Type)[1]	Winter	Early Spring	Late Spring	Early Summer	Late Summer	Fall
Great Horned Owl	(O)			1			
Pileated Woodpecker	(O)		2	4			
Hairy Woodpecker	(P)			22	22	22	
Downy Woodpecker	(P)	22		22	22	22	
Hammond's Flycatcher	(S)			22	22	22	
Dusky Flycatcher	(S)			22	22	22	
Western Flycatcher	(S)			44	22	44	
Western Wood Pewee	(S)			22	22		
Gray Jay	(S)			22	22		
Chestnut-backed Chickadee	(P)	176	44	88	110	198	88
Red-breasted Nuthatch	(P)	66	22	44	22	44	22
Brown Creeper	(P)	44	22	22	22	44	22
Winter Wren	(P)	44	44	44	44	44	44
Varied Thrush	(O)	55					
Hermit Thrush	(S)			22			
Golden-crowned Kinglet	(P)			22	22	22	110
Hutton's Vireo	(S)				22		
Hermit Warbler	(S)			44			
MacGillivray's Warbler	(S)			22	22	22	
Wilson's Warbler	(S)		22	22			
Western Tanager	(S)			44	44		
Black-headed Grosbeak	(S)			22			
Evening Grosbeak	(S)			88			
Pine Siskin	(S)			22			
Red Crossbill	(P)	44	44	66			
Oregon Junco	(P)			44	44	44	88
Song Sparrow	(S)			22			
Total species		7	7	25	16	12	6

[1]P=permanent resident.
S=summer resident.
W=winter resident.
O=occasional resident.

TABLE 6. Percentage of the maximum individual birds in each vegetation type.

Study Area	Winter	Early Spring	Late Spring	Early Summer	Late Summer	Fall
Oak	58.5	57.5	90.9	100.0[1]	43.2	50.4
Fir	43.0	45.7	100.0	68.5	62.7	43.0
Hemlock	55.4	24.6	100.0	62.2	63.8	45.9

[1] The season with the highest total number of individuals was considered 100 percent in each study area.

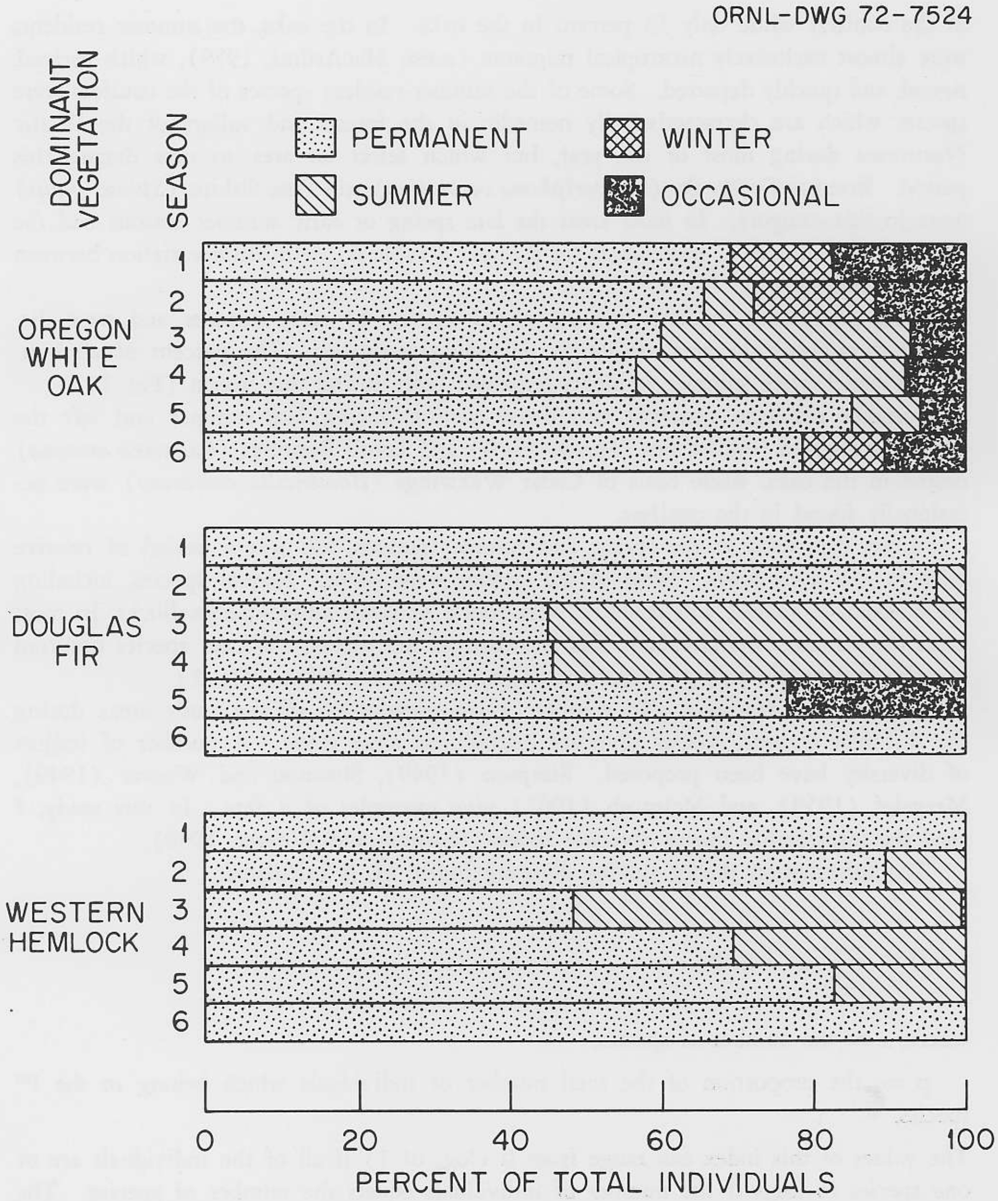

Figure 1. Comparison of residents in vegetation types. Season: 1=Winter, 2=Early Spring, 3=Late Spring, 4=Early Summer, 5=Late Summer, 6=Fall.

territories. Several summer-resident species arrived in all areas (Fig. 1); however, in most areas the total number of individuals decreased as bird species began to spread out (Table 6).

By the beginning of late spring, permanent-resident species were all nesting. During this period, a large influx of summer residents occurred (Fig. 1). There were no longer any winter residents in the oaks, as these species had withdrawn to their coniferous breeding habitats. Summer residents comprised 51 to 55 percent of all individuals in the conifers while only 33 percent in the oaks. In the oaks, the summer residents were almost exclusively neotropical migrants (sensu MacArthur, 1959), which arrived, nested, and quickly departed. Some of the summer-resident species of the conifers were species which are characteristically nomadic in the forests and valleys of the Pacific Northwest during most of the year, but which select an area to nest during this period. Evening Grosbeaks (*Hesperiphona vespertina*) and Pine Siskins (*Spinus pinus*) were in this category. In most areas the late spring or early summer seasons had the highest total number of individuals for the year (Table 6), with little variation between the two seasons.

Most permanent residents had completed nesting by early summer and were dispersed throughout the area, no longer defending territories. The percent of all individuals which were summer residents remained high during this season (Fig. 1).

Summer residents generally completed nesting during late summer and left the forest. American Goldfinches (*Spinus tristis*) and Lazuli Buntings (*Passerina amoena*) nested in the oaks, while nests of Cedar Waxwings (*Bombycilla cedrorum*) were occasionally found in the conifers.

When compared to the spring and summer seasons, fall was a period of relative calm in the study areas. Most of the species were silent. Several species, including the chickadees, juncos, and bushtits, were found in small single-species flocks. In most areas the number of individuals was less than in the winter. Winter species occurred in oak stands while only permanent residents inhabited conifers (Fig. 1).

Diversity of Avifauna. To compare avian populations of the study areas during the different seasons, species diversity calculations were made. A number of indices of diversity have been proposed. Simpson (1949), Shannon and Weaver (1949), Margalef (1959), and McIntosh (1967) give examples of a few. In this study, I used the information theory diversity index (Shannon and Weaver, 1949).

The information theory species diversity index, H, is calculated:

$$H = -\sum_{i=1}^{s} p_i \log_e p_i,$$

where, s = the number of species,

p = the proportion of the total number of individuals which belong to the i^{th} species.

The values of this index can range from 0 ($\log_e$ of 1) if all of the individuals are of one species to $\log_e s$ if the number of individuals equals the number of species. The maximum diversity of a sample is thus given by:

$HMAX = \log_e$.

Comparison of the species diversity, H, of the avifauna in the three vegetation types is shown on a seasonal basis in Table 7. Total diversity was higher in the predominantly oak areas. For late spring, the breeding season for which most diversity indices in the literature have been calculated, the highest diversity (3.21) was obtained in the oaks. Diversity in Douglas-fir dropped to 2.97 and western hemlock rose to 3.07, showing a very close diversity in both conifers. When comparisons of H/HMAX were made (Table 7), the late spring avifaunal diversity indices closely approached HMAX,

TABLE 7. Seasonal species diversity of avifauna in study areas.

Season	H	HMAX	H/HMAX
White Oak			
Winter	2.706	2.996	0.903
Early spring	2.826	3.045	0.928
Late spring	3.210	3.434	0.935
Early summer	3.234	3.434	0.942
Late summer	2.257	2.639	0.855
Fall	2.434	2.833	0.859
Douglas-Fir			
Winter	1.447	1.792	0.808
Early spring	1.718	2.197	0.782
Late spring	2.971	3.219	0.923
Early summer	2.825	2.890	0.977
Late summer	2.110	2.485	0.849
Fall	1.461	1.609	0.908
Western Hemlock			
Winter	1.701	1.946	0.874
Early spring	1.850	1.946	0.951
Late spring	3.070	3.219	0.954
Early summer	2.605	2.773	0.939
Late summer	2.151	2.485	0.865
Fall	1.673	1.792	0.934

indicating that individuals were fairly evenly divided among all species. In fact, during most of the year, the avifaunal diversity of the study areas was relatively close to HMAX. In the majority of comparisons H was at least 90 percent of HMAX.

Discussion

The gradient of vegetation analyzed for avifaunal composition in western Oregon includes three seres of plant community succession (Franklin and Dyrness, 1969). Succession has been defined by Margalef (1969) as "... the occupancy of area by organisms involved in an incessant process of action and reaction which in time results in changes in both the environment and community." He further stated that during succession there was a trend toward increase in biomass, stratification, complexity, and diversity. Odum (1969) listed four types of diversity which could be observed during succession: species variety, expressed as a species number ratio; equitability, the apportionment of individuals among species; stratification; and biochemical diversity, the increase in diversity of organic compounds such as variety of plant pigments. Each of these components of diversity tended to go from low to high in the successional sequence and theoretically reached a stable state in the mature or climax stage. In this study, the measure of equitability species diversity was of primary concern.

If we assumed that species diversity of the avifauna followed the general trend of species diversity in succession, we should expect the bird species diversity of the study areas to increase in accordance with their successional status. Thus, the fir stands should have a higher diversity than the oak, and the hemlock a higher diversity than the fir. Rather, a definite drop in diversity occurred between the oak and fir while only a small rise was noted between the fir and hemlock.

Johnston and Odum (1956) studied the bird populations along a successional gradient in the Piedmont of Georgia and found a bimodal pattern of species abundance; the number of species increased during the early stages of old field succession, declined during early forest stages, and then increased again in the mature forests. Odum (1969) suggested that during succession, an increase in potential niches resulted from increased biomass, stratification, and other consequences of biological organization exceeding the countereffect of increased size and competition of the organisms. While one would assume that diversity should increase for all species of organisms living in an area, this did not necessarily follow. Essentially the assumption was made that as communities became more complex, it became possible for animals to subdivide the area into finer and finer parts, thus reducing the size of niches. In terms of behavior, the animal had become more stereotyped (Klopfer, 1962). When the niche size was reduced, the range of objects in the environment to which the animal responded by feeding, reproducing, seeking shelter, etc. was reduced. As the oak-fir sequence did not follow the expected trend in diversity in relation to avifauna, several factors had to be considered. First, it was possible that a measure of diversity of all organisms of the communities, not just the birds, would have presented the expected increase in diversity with each step in succession. Also, it would have been important to measure the total biomass in the vegetative types to see if any change occurred there.

Second, in examining the three stages in succession, some marked differences in vegetation structure were apparent. The oaks had a much denser understory than undisturbed fir and hemlock communities. This might mean that a larger number of species could be accommodated in the more diverse vegetation.

Finally, the mobility of avian population should be considered when calculating diversity. Patchiness in the vegetation may in itself have accounted for part of the irregular distribution of the avian populations; however, each species of bird had a different ability to move through an area. This movement was influenced by features unique to each species.

When comparison was made with the bird species diversity values obtained in other studies, the results for this study were higher than those reported by MacArthur and MacArthur (1961) for eastern deciduous forests, and also exceeded those from Puerto Rico and all the mature and young tropical forests in Panama (MacArthur, Recher and Cody, 1966). Karr (1968) compared the species diversity in an east-central Illinois strip-mined area during the breeding season and found results in bottomland forests similar to this study. He suggested that the size of the area censused as well as the patchiness in vegetation and patchiness of bird distributions may have influenced the bird species diversity.

Total populations in the study areas in western Oregon were somewhat higher than the avian populations found in eastern forest communities. Johnston and Odum (1956) found 474 individual birds per 100 acres in southern pine and 448 birds per 100 acres in oak-hickory woods. Twomey (1945) reported 406 birds in an elm-maple forest during breeding season. Rohwer and Woolfenden (1969) found 308 birds in a mixed oak woods in Florida. Kendeigh (1944) found a range of 390 to 570 breeding birds per 100 acres in eight deciduous forests of the eastern United States. Bond (1957) recorded 310 to 386 individuals per 100 acres in the upland forests of southern Wisconsin. The range of 154 to 1112 in my study may have been partly the result of the large number of permanent residents in the Oregon forests. During the breeding season in Oregon, the numbers of individuals in the study areas ranged from 464 to 1112. The upper portion of this range exceeded the totals found in eastern forests.

MacArthur (1959) indicated that a very high percent (70-90) of eastern forest species were migratory whereas only 20 to 30 percent of the Oregon forest species were neotropic migrants. My results indicated that 30-55 percent of the birds were summer residents. Oak stands had fewer summer residents (about 35 percent) while the fir and hemlock stands had 50-55 percent. Not all summer residents, however, were neotropic migrants. This was particularly true in the conifers where many nomadic birds settled to breed. In the oaks, the greater proportion of the summer residents were neotropic migrants, the Brown-headed Cowbird (*Molothrus ater*) being one exception. The fact that in the west a lower proportion of the breeding avifauna of an area migrates than in the east may have partially accounted for the relatively high numbers of birds found in the western Oregon forests when compared with eastern studies. The mild winters in the Willamette Valley undoubtedly allowed many bird species to find food during the winter period.

In western Oregon forests, with their rather stable environment and mild winters, a high proportion of the birds were permanent residents. Many of these permanent residents ranged over a wide area in the forests. The forests themselves were distinct, in that communities of upper-story vegetation were separated from each other by narrow ecotones, which contrasted to the many eastern forest communities which shared broad ecotones (Kendeigh, 1948). Much of the forest area in Oregon had been disturbed by man through logging and livestock grazing. Natural events such as windfall had disturbed other areas. Thus, there were "gap phases" within the forested areas. In this study, avian community structure did not conform to the plant community outline. There were some birds that might be classified with a deciduous or coniferous community (*e.g.,* Black-capped Chickadee (*Parus atricapillus*) and White-breasted Nuthatch (*Sitta carolinensis*) in the former and Chestnut-backed Chickadee (*Parus rufescens*) and Red-breasted Nuthatch (*Sitta canadensis*) in the latter. Still, most birds did not confine themselves to either type of plant community, as was shown by juncos, creepers, and towhees. During the nonbreeding seasons, particularly, birds seemed less subjected to the confines of a particular plant community. All of the winter residents in the oaks were found as permanent residents in the conifers.

Summary

The avifaunal composition of 10 western Oregon forest stands located at the eastern base of the Coast Range was examined on a seasonal basis. The stands were dominated by Oregon white oak, Douglas-fir, and western hemlock. Avian populations were sampled monthly from January 1968 to January 1970, using permanent transects.

Oak-dominated stands had the highest bird species diversity in all seasons. This is in contrast to the expected increase in diversity with each successional sere. In most cases the actual species diversity was at least 90 percent of the maximum possible diversity.

All fir and hemlock stands shared a large number of species and supported roughly similar total populations. In the ecotonal areas, diversity was slightly higher than in the surrounding pure stands of either deciduous or coniferous vegetation.

More individuals and species were found in western Oregon forests than reported for forests in eastern United States. Further, a large proportion of the Oregon birds were permanent residents. The percentage of migratory birds was lower than in eastern forests because of this large number of permanent residents. These differences may in part stem from the milder winter climate characteristic of western Oregon.

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Literature Cited

Anderson, S. H. 1970. The avifauna composition of Oregon white oak. Condor 72: 417-423.
Bond, R. R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. Ecol. Monogr. 27: 351-384.
Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecol. 37: 451-460.
Forbes, S. A., and A. Gross. 1923. On the numbers and local distribution of Illinois land birds of the open country in winter, spring, and fall. Bull. Illus. Natur. Hist. Surv. 14: 397-453.
Franklin, J. F., and C. T. Dyrness. 1969. Vegetation of Oregon and Washington. U.S. Dept. Agr. Forest Service Research Paper PNW-80.
Johnston, D. W., and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecol. 37: 50-62.
Karr, J. R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. Condor 70: 348-357.
Kendeigh, S. C. 1944. Measurement of bird populations. Ecol. Monogra. 14: 67-106.
——————. 1948. Bird populations and biotic communities in northern lower Michigan. Ecol. 29: 101-114.
Klopfer, P. H. 1962. Behavioral Aspects of Ecology. Prentice Hall, Englewood Cliffs, New York. 166 pp.
MacArthur, R. H. 1959. On breeding distribution pattern of North American migrant birds. Auk 76: 318-325.
——————, and J. W. MacArthur. 1961. On bird species diversity. Ecol. 42: 594-598.
——————, H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. Amer. Natur. 100: 319-332.
McIntosh, R. P. 1967. An index of diversity and the relation of certain concepts to diversity. Ecol. 48: 392-404.
Margalef, D. R. 1958. Information theory in ecology. General Systems 3: 36-71.
——————. 1968. Perspectives in Ecological Theory. Univ. of Chicago Press, Chicago. 111 pp.
Odum, E. P. 1969. The strategy of ecosystem development. Sci. 164: 262-270.
Rohwer, S. A., and G. E. Woolfenden. 1969. Breeding birds of two Florida woodlands: Comparisons with areas of north of Florida. Condor 71: 38-48.
Shannon, C., and W. Weaver. 1949. The Mathematical Theory of Communication. Univ. of Illinois Press, Chicago. 117 pp.
Simpson, E. H. 1949. Measurement of diversity. Nature 163: 688.
Twomey, A. C. 1945. The bird population of an elm-maple forest with special reference to aspection, territorialism and coactions. Ecol. Monogra. 15: 173-205.

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