BIRD COMMUNITIES IN THE CONIFEROUS FOREST BIOME

By DANA PAUL SNYDER

The tendency of organisms to form more or less distinct biotic groupings has led to many attempts at classification of such units. The early classifications dealing with North America have been summarized by Merriam (1892), who in turn proposed the life-zone system based on the distribution of both plants and animals (1890). Daubenmire (1938) has summarized the important criticisms of the life-zone concept. Dice (1943) has recently developed the idea of the "biotic province" as an aid in the classification of ecological communities. Each province has a continuous geographic distribution and is regarded as an evolutionary unit. Since the concept has not yet been widely applied, it cannot be properly evaluated.

Perhaps the most useful classification of communities at the present time is that developed by Clements and Shelford (1939). In this system the largest natural unit, identified by the life form of the climax dominant vegetation, is called the biome. Important in this system is the recognition of developmental or seral communities as distinct from the climax community. Another emphasis of this system is upon the abundant or otherwise significant organisms rather than the uncommon species.

The biome concept is undergoing still further development. From a study of biome maps one is likely to infer that the communities within each biome are always more closely related to each other than to communities in other biomes. Such is not always true. For example, deciduous forest may occur as a developmental community within the coniferous forest biome. The plant and animal constituents of such a deciduous forest often have more in common with the deciduous forest biome than with the climax coniferous forest community. This situation was pointed out for birds by Pitelka (1941). Kendeigh (1948) has introduced a subdivision, the *biociation,* into the biome classification that takes care of these inter-biome relations. The biociation is an animal community of definite taxonomic composition occurring in vegetation of a uniform type of life-form. Such a community may be climax in one biome, but seral, a *biocies,* in another.

The present study was undertaken to investigate the organization of bird communities within the coniferous forest biome. Breeding bird populations were measured in three vegetation types of the coniferous forest during the summer of 1947, in the vicinity of Science Lodge, the biological station of the University of Colorado. This station is situated just east of the continental divide in Boulder County and is approximately 21 miles west of the city of Boulder, Colorado.

The writer wishes at this point to express his appreciation to Dr. S. C. Kendeigh of the University of Illinois under whose direction this work was carried out. His suggestions and corrections have been of great assistance in compiling data and completing the manuscript. The writer is indebted to Dr. Gordon Alexander of the University of Colorado for suggestions and supervision of the field study. Thanks are due the University of Colorado for the use of equipment. The aerial photographs are from the files of the Forest Service. The map is redrawn from the Forest Service map of Arapahoe National Forest, 1938.

BIRD POPULATIONS

Procedure.—Study plots for censusing breeding birds were set up in three forest communities, each community characterized by different plant dominants. The plots varied in size and shape as a result of difficulty in finding representative sites.

The climax montane forest in this region is dominated by ponderosa pine, *Pinus ponderosa,* and Douglas fir, *Pseudotsuga taxifolia.* There are two shrub layers, chiefly

Juniperus communis and *Arctostaphylos uva-ursi,* prostrate on the forest floor, and *Ribes, Jamesia, Ceanothus,* and other shrubs, growing erect. The montane forest is open, and therefore a number of grasses, sedges, and forbs are found. The community in this part of the Rocky Mountains extends from an elevation of about 5400 feet to approximately 8400 feet on north-facing slopes and 9500 feet on south-facing slopes. The two dominant species tend to separate into consociations at certain points, the pine inhabiting the drier situations and the Douglas fir the moister spots.

The climax subalpine forest is dominated by subalpine fir, *Abies lasiocarpa,* and Engelmann spruce, *Picea engelmanni.* In certain exposed rocky areas these dominants are replaced by limber pine, *Pinus flexilis.* The lower shrub stratum is composed chiefly of scattered stands of *Vaccinium.* This community extends from the upper border of the montane forest up to 10,500 feet in this part of Colorado.

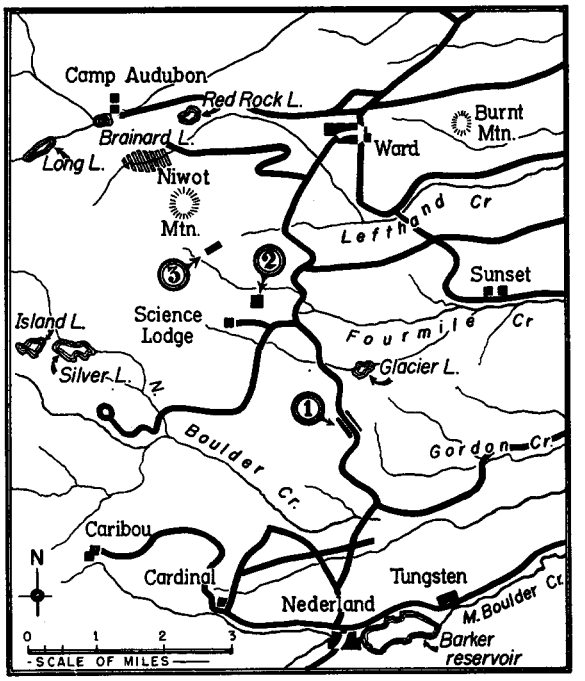

Fig. 7. Location of census plots in Boulder County, Colorado. 1, Douglas fir-ponderosa pine; 2, lodgepole pine; 3, Engelmann spruce-subalpine fir. Roads represented by heavy black lines.

Since Lodgepole pine, *Pinus contorta,* occurs in both the subalpine and the montane forests and since it frequently remains as a subclimax for a great length of time, it forms an important forest community. Therefore, an intermediate census area was selected in a nearly pure stand of this species for comparison with the other two communities which have two species as dominants.

Plot 1, in the montane forest, measured 200 by 450 meters which made an area of 9 hectares (22.2 acres). It was situated at an elevation of 8800 feet. A number of lodgepole pine trees and a few stands of aspen were scattered among the ponderosa pine and Douglas fir. A road ran through the long section of the plot which decreased the area

actually covered with forest. However, no correction was made in the size of the census area as many of the birds made use of the space. Plot 2, situated at an elevation of 9500 feet in the lodgepole pine forest, was 300 by 300 meters, making an area of 9 hectares (22.2 acres). Young trees predominated and formed very thick stands over parts of the area, although small openings occurred in a few places. Limber pines were present along the north edge of the area, and a very few were scattered throughout the plot. Plot 3, in the subalpine forest, was 150 by 400 meters or 6 hectares (14.8 acres) in area. The effective census area, however, was only 5¾ hectares (14.2 acres), since a meadow 50 by 50 meters occurred along one edge. The plot was located at an elevation of 10,200 feet. It contained a stand of limber pine in one corner which accounted for about 20 per cent of the canopy, the remainder being made up of the dominants of spruce and fir.

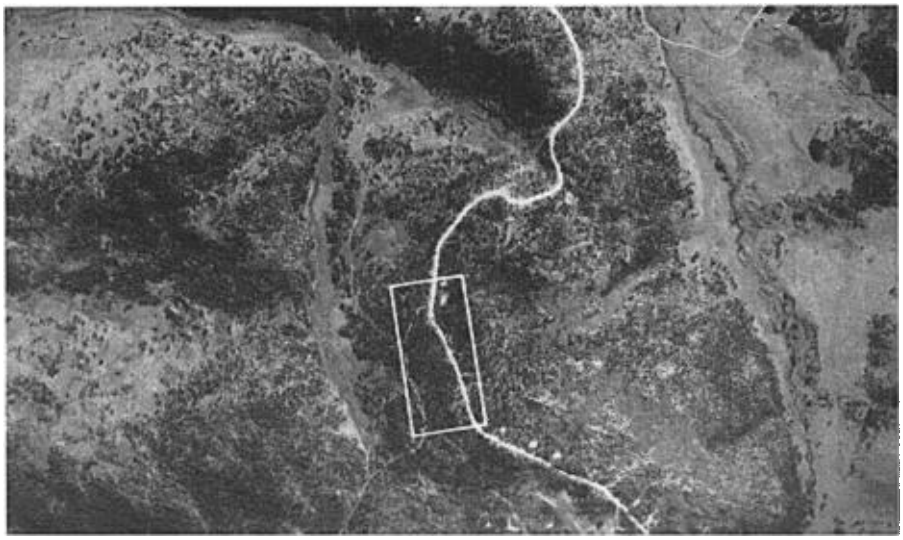

Fig. 8. Aerial view of plot 1, the Douglas fir-ponderosa pine forest. Top of photograph is north.

The plots were laid out in the form of grids by pacing with a compass. The intersections at 50 meter intervals were marked by blazing and assigned numbers. Thus, any point within the plot could be quickly located on a map of the area. The locations of the various areas are shown in figure 7. The location of each plot in relation to the surrounding topography is shown by aerial photographs, figures 8, 9, and 10. On each photograph the census plot is enclosed by white lines.

The bird census was taken by traversing back and forth over the entire plot, keeping between two adjacent blazed lines. When a bird was seen or heard, it was spotted on a map of the census plot. After each plot had been covered five times, individual maps were made for each species so that the approximate boundaries of the territories, and thus the number of breeding pairs, could be counted (Kendeigh, 1944). These figures were then converted into the number of pairs per 100 acres (40 hectares). Species with less than one-half of a territory were listed with a plus but not counted in the total number of pairs present. When a number of partial territories of a species extended into the plot, they were added together. The density of each species is given to the nearest whole number.

The last major snowfall of the season occurred on June 11 and 12. A small amount

of snow fell on June 22. Censusing was begun on June 23 and lasted until July 31. Censuses were usually taken from daybreak to 10 or 11 a.m. but a few were made later in the day. Nesting was well under way at the time censusing began. The Canada Jay, Steller Jay and Clark Nutcracker had apparently completed nesting activities, so

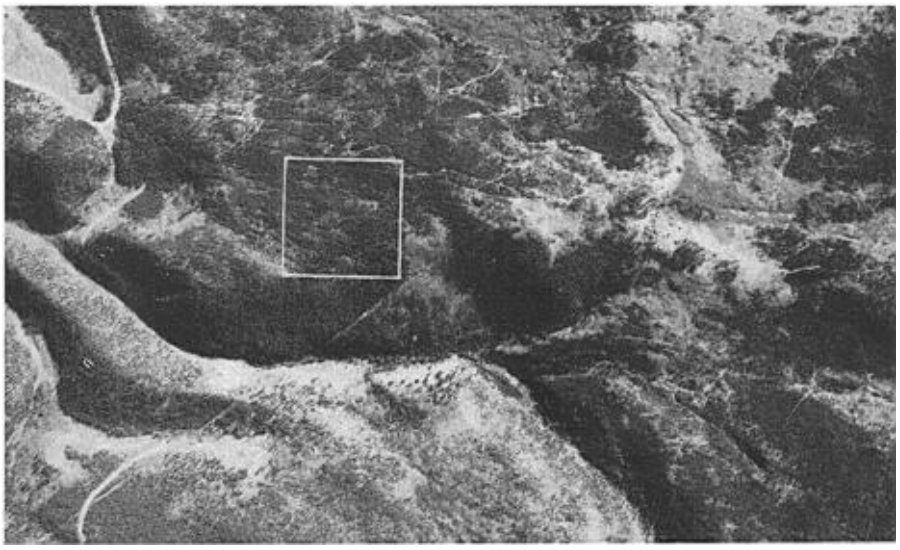

Fig. 9. Aerial view of plot 2, the lodgepole pine forest. Top of photograph is south.

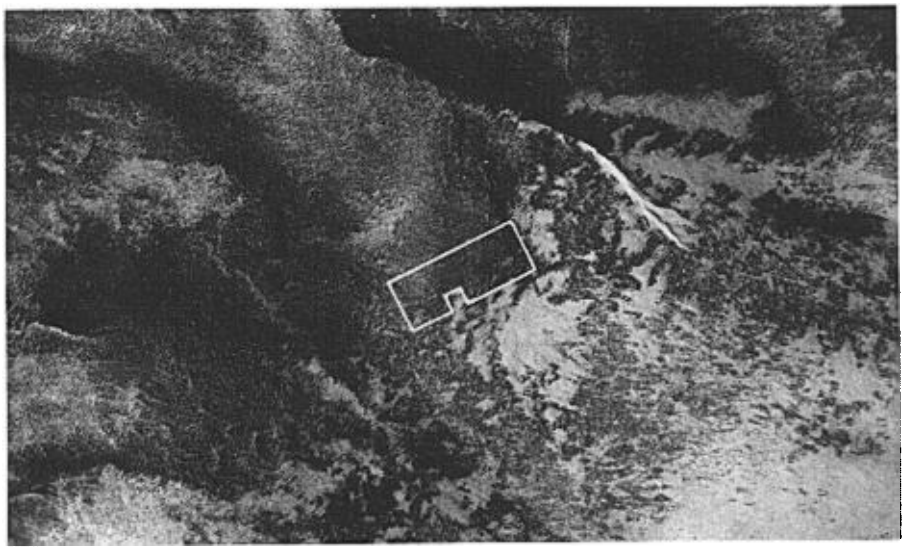

Fig. 10. Aerial view of plot 3, the Engelmann spruce-subalpine fir forest. Top of photograph is south.

that their abundance could not be ascertained. The population figures for the Pine Siskin are based on the frequent observation of single individuals often in flight. The density as given is apparently higher than normal for the species but is believed to indicate fairly closely the actual population in the summer of 1947.

Census results.—The breeding populations of the birds are summarized in table 1. The Goshawk, Red-tailed Hawk, Prairie Falcon, and Raven were seen in the region but not frequently enough to obtain an estimate of their populations. When the three forest communities are considered together, the best represented families in number of species are the Fringillidae, the Turdidae, and the Corvidae. However, on the basis of individuals, the families stand in the order: Fringillidae, Sylviidae, Turdidae, and Paridae. Other families are represented by much smaller numbers of individuals. When the number of individuals is considered for each plot separately, the order of abundance is similar, except for the entire absence of the Sylviidae in the lodgepole pine forest.

Table 1
Breeding Birds of the Coniferous Forest in Colorado

	Actual counts			Density per acres (40 hectares)		
	Plot 1 Douglas fir—ponderosa pine	Plot 2 Lodge-pole pine	Plot 3 Engelmann spruce—subalpine fir	Plot 1 Douglas fir—ponderosa pine	Plot 2 Lodge-pole pine	Plot 3 Engelmann spruce—subalpine fir
	9 ha.	9 ha.	5.75 ha.			
Sharp-shinned Hawk, *Accipiter striatus*	+	0	0	+	0	0
Dusky Grouse, *Dendragapus obscurus*	0	+	1—	0	+	4
Mourning Dove, *Zenaidura macroura*	+	0	0	+	0	0
Nighthawk, *Chordeiles minor*	0	1+	0	0	5	0
Broad-tailed Hummingbird, *Selasphorus platycercus*	1+	0	0	5	0	0
Red-shafted Flicker, *Colaptes cafer*	0	+	+	0	+	+
Hairy Woodpecker, *Dendrocopos villosus*	+	0	1	+	0	7
Canada Jay, *Perisoreus canadensis*	0	+	0	0	+	0
Steller Jay, *Cyanocitta stelleri*	0	+	0	0	+	0
Clark Nutcracker, *Nucifraga columbiana*	+	+	+	+	+	+
Mountain Chickadee, *Parus gambeli*	3—	2	2—	12	9	12
Red-breasted Nuthatch, *Sitta canadensis*	+	0	0	+	0	0
Brown Creeper, *Certhia familiaris*	+	0	0	+	0	0
Robin, *Turdus migratorius*	2—	+	0	8	+	0
Hermit Thrush, *Hylocichla guttata*	2	3	1+	9	13	8
Townsend Solitaire, *Myadestes townsendi*	0	+	+	0	+	+
Ruby-crowned Kinglet, *Regulus calendula*	4	0	4—	18	0	28
Audubon Warbler, *Dendroica auduboni*	1	+	1—	5	+	6
Pine Grosbeak, *Pinicola enucleator*	0	0	1—	0	0	4
Pine Siskin, *Spinus pinus*	2	5+	4—	9	23	25
Red Crossbill, *Loxia curvirostra*	+	1	+	+	4	+
Gray-headed Junco, *Junco caniceps*	8	1+	+	36	5	+
				102+	59+	94+

+ Indicates density below one-half pair.

The density of breeding pairs for the montane, the subalpine, and the lodgepole pine forests are 102+, 94+, and 59+, respectively. The density for the subalpine forest is low compared with similar forests in the east. Kendeigh (1947) found 319+ pairs per 100 acres near Black Sturgeon Lake in Ontario, Cadbury and Cruickshank (1947) listed 273 pairs per 100 acres on Hog Island off the coast of Maine, and DeGarmo (1948) gives 313+ pairs per 100 acres (two year average) for young spruce in West Virginia. The Ontario census was carried out during a spruce budworm outbreak which probably accounted for the large population there. The present findings agree more nearly with the figures of 79 pairs per 100 acres given by Palmgren (1930) for spruce forests in Finland and with those of 94 pairs per 100 acres given by Soveri (1940),

who also worked in Finland. However, Hayward (1948) reported a high summer bird population of 16.5 individuals per hectare (330 pairs ? per 100 acres) in the subalpine forest in Utah. In the montane forest in Utah he reported 15.5 individuals per hectare (310 pairs? per 100 acres) as the summer bird population. These figures were apparently estimated by means of cruising over measured areas usually 5 acres in extent. Such estimations, especially from small areas, often tend to result in population figures which are above the actual breeding density. Hering (1948) in a study of the bird population of the Black Forest in Colorado, which is predominantly ponderosa pine, found 96 pairs per 100 acres.

Discussion.—It is evident from table 1 that the four families (Fringillidae, Sylviidae, Turdidae and Paridae) with the most individuals are fairly well distributed among the three study areas. Furthermore, three of the five most abundant species are found in each of the three areas. In these cases the bird community did not change with the plant species but appeared correlated with the life form of the vegetation. The Ruby-crowned Kinglet, however, did not nest in the lodgepole pine plot, although this forest was intermediate in elevation between the subalpine forest and the montane forest, in each of which the bird was abundant. Apparently some feature of its niche was lacking. The junco occurred on plots 1 and 2, but at the elevation of the subalpine forest the birds were restricted to the edge conditions. In the two lower areas more edge existed within the census plots. It appears that this species is also reacting to the structure of the vegetation.

Thus, each species occupies its niche, even when it occurs in more than one plant community regardless of the species composition of plant dominants. Hayward (1945), in a study of coniferous forests in Utah, found a similar close biotic relationship between the montane and the subalpine forest. He found that almost 100 per cent of the mammal and 61 per cent of the bird species occurred through both forests. This correlation of animal communities with plant-life forms was apparently realized by some of the earlier workers (see Carpenter, 1939) although first clearly stated by Shelford (1913:307, 308) and Vestal (1913:13;1914:430).

COMMUNITY ORGANIZATION OF BIRDS

Bird distribution in the coniferous forest.—Kendeigh (1948) has recently recognized two biociations and five biocies in eastern North America. The climax and late seral plant stages of the coniferous forest, along with their constituent animals, constitute one biociation. Equivalent stages in the deciduous forest make up the other biociation. Each community has characteristic species which are adjusted to the respective vegetation types and which follow these types closely when occurring in mixed stands or ecotones.

In order to determine whether the coniferous forest biociation of the coniferous forest in the east is the same in the Rocky Mountains a comparison of the breeding bird population was made in table 2. Since this biociation includes only those species which occur in forests of relatively dense stands of trees and excludes those which require open forests or forest-edge conditions, these latter have for the most part been eliminated from the table as they really belong to the forest-edge biocies. The classification of only a few species offered any special difficulties. The breeding bird population for the Rocky Mountain region is the average of the three stations discussed in this paper. The population of the forest community in Ontario was determined by Kendeigh (1947). The area censused is situated about 90 miles north of Port Arthur, Ontario. This virgin forest is composed of 37 per cent balsam fir, 26 per cent black spruce, 6 per cent white spruce, 4+ per cent white cedar, jack pine, and tamarack, 23 per cent white birch, and 2 per

Table 2

Breeding Birds in the Climax Coniferous Forest

Community		Density per 100 acres (40 hectares)		
	Rocky Mountain coniferous forest		Eastern coniferous forest	
			Western Ontario	Maine
Dusky Grouse, *Dendragapus obscurus*	PR	1		
Franklin Grouse, *Canachites franklinii*	PR	*		
Williamson Sapsucker, *Sphyrapicus thyroideus*	LM	*		
Hammond Flycatcher, *Empidonax hammondii*	LM	*		
Steller Jay, *Cyanocitta stelleri*	PR	+		
Clark Nutcracker, *Nucifraga columbiana*	PR	+		
Mountain Chickadee, *Parus gambeli*	PR	11		
Chestnut-backed Chickadee, *Parus rufescens*	PR	*		
White-breasted Nuthatch, *Sitta carolinensis*	PR	*		
Pigmy Nuthatch, *Sitta pygmaea*	PR	*		
Varied Thrush, *Ixoreus naevius*	LM	*		
Townsend Warbler, *Dendroica townsendi*	LM	*		
Grace Warbler, *Dendroica graciae*	LM	*		
Goshawk, *Accipiter gentilis*	PR	*	+	*
Sharp-shinned Hawk, *Accipiter striatus*	PR	+	*	*
Horned Owl, *Bubo virginianus*	PR	*	*	*
Great Gray Owl, *Strix nebulosa*	PR	*	*	
Arctic Three-toed Woodpecker, *Picoïdes arcticus*	PR	*	2	*
Three-toed Woodpecker, *Picoïdes tridactylus*	PR	*	+	*
Olive-sided Flycatcher, *Nuttallornis borealis*	LM	*	*	*
Canada Jay, *Perisoreus canadensis*	PR	+	4	*
Hudsonian Chickadee, *Parus hudsonicus*	PR	*	2	*
Red-breasted Nuthatch, *Sitta canadensis*	PR	+	3	+
Brown Creeper, *Certhia familiaris*	PR	+	9	*
Winter Wren, *Troglodytes troglodytes*	PR	*	5	*
Hermit Thrush, *Hylocichla guttata*	LM	10	1	3
Golden-crowned Kinglet, *Regulus satrapa*	PR	*	8	23
Ruby-crowned Kinglet, *Regulus calendula*	LM	15	2	*
Solitary Vireo, *Vireo solitarius*	LM	*	2	*
Evening Grosbeak, *Hesperiphona vespertina*	PR	*	*	
Pine Grosbeak, *Pinicola enucleator*	PR	1	*	*
Pine Siskin, *Spinus pinus*	PR	19	1	*
Red Crossbill, *Loxia curvirostra*	PR	+	*	*
White-winged Crossbill, *Loxia leucoptera*	PR	*	*	*
Broad-winged Hawk, *Buteo platypterus*	LM		+	*
Pigeon Hawk, *Falco columbarius*	LM		+	*
Spruce Grouse, *Canachites canadensis*	PR		1	*
Black-capped Chickadee, *Parus atricapillus*	PR		2	9
Swainson Thrush, *Hylocichla ustulata*	LM		4	12
Tennessee Warbler, *Vermivora peregrina*	LM		59	*
Parula Warbler, *Parula americana*	LM		*	34
Magnolia Warbler, *Dendroica magnolia*	LM		6	26
Cape May Warbler, *Dendroica tigrina*	LM		28	4
Black-throated Green Warbler, *Dendroica virens*	LM		6	37
Blackburnian Warbler, *Dendroica fusca*	LM		6	15
Bay-breasted Warbler, *Dendroica castanea*	LM		92	1

Asterisk indicates occurrence of the species in the community but not on the census plot; PR, permanent resident or altitudinal migrant; LM, latitudinal migrant.

The list for the Rocky Mountains is compiled from various sources and pertains to areas from southern Canada southward; some species occur only in parts of this region.

cent quaking aspen. The figures for the Maine community are from the censuses (nine-year average) made by Cadbury and Cruickshank (1947) at Hog Island off the coast of Maine. The area consists of 25 acres of climax spruce and five partially cleared acres with buildings and young growth.

A study of table 2 shows that many species occur over a wide range within the coniferous forest. Those species which are found more or less throughout the coniferous forest comprise 46 per cent of the total. Such birds as the Golden-crowned Kinglet, Ruby-crowned Kinglet, Red-breasted Nuthatch, Olive-sided Flycatcher, and others tend to tie together the various parts of the biome. Many species are, however, restricted in regard to east-west distribution. Of the 46 species listed, 26 per cent are recorded only in the eastern two stations and another 28 per cent are listed only for the Rocky Mountain area. It appears that the species composition of birds in Ontario and Maine is essentially similar and that it differs markedly in the Rocky Mountains.

Table 3

Zoogeographic Origin of Breeding Birds in the Climax Coniferous Forest

	Percentage composition of population							
	Old World		North American		South American		Unanalyzed	
	species	pairs	species	pairs	species	pairs	species	pairs
Rocky Mountains	65	98	17	2	6	....	12	....
Ontario and Maine	52	20	30	79	3	....	15	1

Zoogeographic origin of the coniferous forest birds.—An analysis of the zoogeographic origin of the populations also indicates a difference between those of the Rocky Mountains and those of the more eastern forests (table 3). The data for Ontario and Maine are combined, and their population figures are averaged. The two communities are then analyzed both on the basis of breeding species and of breeding pairs. The place of origin of the various groups are taken from Mayr (1946). For most species this is based on the origin of the family. In a few cases the genus is used. For the Fringillidae the origin of the species is based on the subfamily to which it belongs. Four categories are used: Old World, North American, South American, and unanalyzed, the latter representing groups for which reliable interpretation of origin have not yet been obtained. The two types of analyses, by species and by pairs, are not entirely comparable. The analysis by pairs is based only on the actual communities censused while the analysis by species includes all that are listed in table 2. Obviously, these figures for pair analysis, representing only three localities, are indicative only and should not be considered as absolute values.

The South American element is relatively unimportant and will not be considered further in the present discussion. The analysis on the basis of breeding pairs shows an almost exclusive Old World element in the Rocky Mountain forests and a predominant North American element in the eastern forests. On the basis of species these differences are still evident although statistically they are not so extreme. Apparently the Old World forms in the east are not able to build up as high populations as do the North American forms. This may be because of the competition which they meet there with the high populations of North American parulids.

In the different plant communities in the Rocky Mountains the proportion of Old World birds in the population shows a correlation with elevation (fig. 11). Data for station 1 are from a census by Longley (1944) of a western hemlock-Douglas fir forest

near Bayview in northern Idaho. The data for station 2 are from a census by Hering (1948) of ponderosa pine in the Black Forest, Colorado. The data for stations 3, 4, and 5 are from the Colorado censuses described in this paper. The entire bird populations are included in this analysis, although some stations include a mixture of other vegetation types. From figure 11 it can be seen that the increase in Old World elements in the populations corresponds to an increase in altitude.

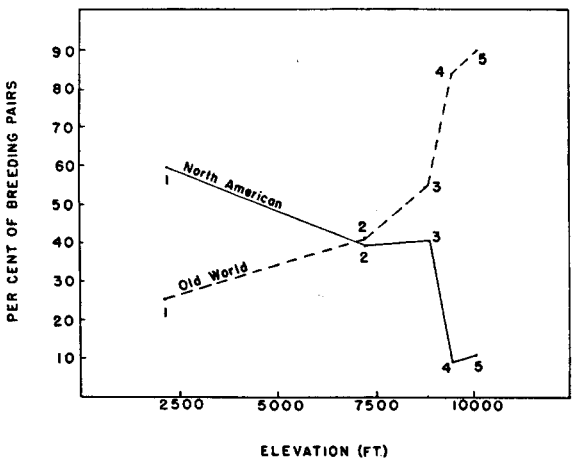

Fig. 11. Relation between numbers of pairs of species of Old World origin and those of North American origin in western forests at various elevations. 1, western hemlock-Douglas fir (Idaho); 2, ponderosa pine (Colorado); 3, Douglas fir-ponderosa pine (Colorado); 4, lodgepole pine (Colorado); 5, Engelmann spruce-subalpine fir (Colorado).

Station 1, according to the description by Longley, apparently has the greatest amount of deciduous growth. The relative amounts of coniferous and deciduous vegetation for station 2 are not available. The percentage of coniferous vegetation in the communities increases gradually from station 3 up to station 5. It is evident that the increase in the amount of coniferous vegetation with altitude is correlated with the increase of the Old World element in the bird populations. The influence of the altitude in producing this result may be partially, at least, an indirect one, its effect being to cause a change in the vegetation. When the influence of the vegetation is removed by analyzing only the coniferous forest birds, the Old World element (breeding pairs) shows an occurrence of 64 per cent at station 1, 53 per cent at station 2, 100 per cent at station 3, 100 per cent at station 4, and 80 per cent at station 5. Mayr (1946) has pointed out that the Old World element decreases on the continent from north to south, and the above figures extend this principle to a decrease also with decreasing altitude.

The Old World element was also shown by Mayr (1946) to be composed in large part of non-migratory birds, which probably had become adapted to cold during development in Asia and later invasion into North America from the north. Of the coniferous forest species occurring in the Rocky Mountains (table 2), 74 per cent are either permanent residents or move only to lower elevations in the winter. In the particular communities censused in Colorado these cold-adapted species made up 56 per cent of the breeding pairs. Thus, the latitudinal migrants, the non-cold adapted birds which move south

during the winter, comprise less than one-half of the breeding population. In Ontario and Maine, on the other hand, only 58 per cent of the species are permanent residents, and in the communities censused they contributed only 17 per cent of the breeding population. Certain migratory birds, such as the Golden-crowned Kinglet, have been placed in the resident group for the purpose of these calculations because the species by wintering in temperate or cold-temperate regions indicate adaptation to cold. Thus, in this respect, they are more similar to the non-migrants than to the migrants.

Eastern North America, perhaps because it was farther from the Alaskan land bridge or for other reasons, may not have received the Old World forms dispersing from Siberia as early as did the west. Such a situation would leave the east more available for indigenous elements and for invasion of South American groups. Since neither of these were primarily cold adapted groups, many of the species would have to assume a migratory habit to occupy the colder parts of the continent, while most of the Old World birds which came into the area would be cold adapted and could become permanent residents (see Mayr, 1946). The probable separation of the eastern and western coniferous forest during Pleistocene glaciation (Rand, 1948) may possibly have effected some differentiation between the avifaunas of the two regions. Factors such as these may account for the differences between the avian communities of the east and of the Rocky Mountain region.

Discussion.—The climax bird communities in the Rocky Mountains and in eastern North America differ in three important respects: (1) species composition, (2) zoogeographic origin, and (3) migratory status. Therefore, these regions represent two distinct biociations within the coniferous forest biome. The eastern community has been named and described by Kendeigh (1948) as the *Dendroica-Regulus* coniferous forest biociation. The western community may tentatively be distinguished as the *Parus-Spinus* coniferous forest biociation, after the Mountain Chickadee and Pine Siskin.

SUMMARY AND CONCLUSIONS

Censuses of breeding birds were carried out in three plant communities in the Rocky Mountains of Colorado. The populations per 100 acres (40 hectares) were: 102+ pairs in Douglas fir and ponderosa pine, 94+ pairs in Engelmann spruce and subalpine fir, and 59+ pairs in lodgepole pine. The most abundant species were the Mountain Chickadee, Ruby-crowned Kinglet, Hermit Thrush, Pine Siskin, and Gray-headed Junco, and all except the kinglet occurred in each of the three communities.

In the Rocky Mountains, an increase in elevation is correlated with an increase in birds of Old World origin and a decrease in birds of North American origin. This correlation is apparently brought about, in part, by the increase in the percentage of coniferous forest and the decrease in the percentage of deciduous forest in the vegetation at higher elevations.

In the climax coniferous forest community in the Rocky Mountains most of the breeding pairs are of species of Old World origin and are in large part permanent residents. In the east the North American element is in the majority, and the birds are largely migratory.

The distribution, zoogeographic origin, and migratory status of the breeding populations indicate that at least two distinct climax avian communities occur in the coniferous forest biome of North America. The Rocky Mountain community is named the *Parus-Spinus* coniferous forest biociation after the Mountain Chickadee and the Pine Siskin to distinguish it from the *Dendroica-Regulus* coniferous forest biociation of eastern North America.

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