AN ANALYSIS OF AVIFAUNAS IN THE TETON MOUNTAINS AND JACKSON HOLE, WYOMING

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Faunal analyses may be made for several purposes: to reveal ecologic characteristics of a community either of present times or, as is done by paleontologists, of past ages (Miller, 1937); to demonstrate pathways of energy exchange within an ecosystem (Turcek, 1952); or to evaluate ecological or evolutionary relationships between faunas (Miller, 1955; Snyder, 1950; Corti, 1952). The present analysis is an effort to secure results useful for all three. The primary object was to collect data on the bird life of an area in the Rocky Mountains for comparison with that of the Sierra Nevada. Results of the comparison will appear in a latter report on Sierran avifaunas. Herein are reported findings on community characteristics and trophic or feeding relationships as determined from analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming.

The work was done during the summers of 1952 and 1954 at the Jackson Hole Biological Station of the University of Wyoming, where facilities were kindly provided. Financial support was generously given by the New York Zoological Society for which I am grateful. I also wish to express my thanks for assistance to Mr. James Simon, former director, Dr. L. Floyd Clarke, present director of the station, and my colleagues and friends at the station. The weights used were taken from specimens in the Museum of Vertebrate Zoology at Berkeley; to Dr. A. H. Miller and Dr. F. A. Pitelka I express my gratitude for permission to use this material.

DESCRIPTION OF THE AREA

The Teton Mountains form the west wall of the valley of Jackson Hole in northwestern Wyoming. They rise abruptly from the valley floor (6900 feet) to peaks of 10,000 to 13,766 feet. The canyons, running at right angles to the axis of the range, are deep glaciated troughs draining eastward into a row of moraine-enclosed lakes along the base of the Tetons. The lower parts of the mountains and the canyons are forested up to about 10,000 feet, but avalanches, cliffs and talus slides make the distribution of vegetation varied and irregular. Alpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Douglas fir (*Pseudotsuga taxifolia*) dominate at lower elevations; white-bark pine (*Pinus albicaulis*) dominates at higher elevations.

Jackson Hole is a narrow valley extending about forty-eight miles north and south; its greatest width is about twelve miles. The northern end is filled with the dammed waters of Jackson Lake from which the Snake River runs southwestward the length of the valley. The northern and eastern flanks of the valley are formed by the Yellowstone and Mount Leidy highlands while the Gros Ventre and Hoback mountains enclose the southern end. There are three towns: Moran at the northern end where the Biological Station is located, Jackson at the southern end, and Moose halfway between them. The predominant vegetation of the valley floor, sagebrush (*Artemisia tridentata*), is interrupted by groves of aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*) forests, and, where the beavers have dammed the streams, willow (*Salix*) swamps. An association characterized by southern poplar (*Populus deltoides*) and blue spruce (*Picea pungens*) exists along the banks of the Snake River. Hills within the valley and around its margin are forested. The floristics of most of the vegetation types in the area have been studied in detail by Reed (1952). A more thorough description of the area may be found in papers by Fryxell (1938) and James (1936), and the geology and glacial history of the valley is dealt with in a paper by Fryxell (1930). Nearly all the area is now included in Grand Teton National Park.

During early summer the climate alternates between sunny days and thunderstorms that last several days. Freezing nights are not uncommon in late June. As the summer progresses, rainstorms sometimes become less frequent and freezing nights are rare or lacking. Maximum daytime temperatures are usually between 70 and 80 degrees F.

METHODS

In this study censuses were made by the strip-transect method. Birds were counted in four communities in Indian Paintbrush Canyon in the Tetons and in three vegetation types in the valley near the Biological Station. The strips were between one-half and one mile long, depending on how large a pure stand of the vegetation type could be found. In all instances the strips were sixty yards wide. Distances of thirty yards on either side of the route were paced off at intervals along the strip. I walked along the route at a rate of about one mile per hour recording each bird seen or heard within the strip. Notes on activity were made on birds seen. Counts were made during the morning hours, usually between 7:00 and 10:00 a.m.

There were several reasons for using this method in preference to plotting territories of singing males in a measured area: (1) The Sierran censuses with which these data were to be comparable were made on strip transects; (2) the irregular vegetation and rugged terrain make traversing a quadrat, assuming one large enough could be laid out, an exercise in mountaineering; and (3) the breeding seasons of the birds are not synchronized and some such as the Clark Nutcracker are finished before others have begun.

In the Rockies of Colorado twenty-one miles west of Boulder, Snyder (1950) censused in lodgepole pine and spruce-fir forests. Mapping territories in quadrats of 14.2 to 22.2 acres, he was able to get specific density figures for about half the species present. Although there are undoubtedly differences in climate and soil between that area and the Tetons, a comparison of the two regions is presented in table 1 in terms of birds per 100 acres.

Table 1

A Comparison of Densities of Birds in Two Areas of Coniferous Forest

Habitat	Species	Area: Colorado	Area: Wyoming
Lodgepole pine forest	Mountain Chickadee	9/100 ac.	6.7/100 ac.
	Siskin	23	1.7
	Junco	5	10.0
Spruce-fir forest	Hairy Woodpecker	7	2.8
	Mountain Chickadee	12	7.0
	Hermit Thrush	8	3.5
	Ruby-crowned Kinglet	28	8.4
	Audubon Warbler	6	7.7
	Pine Grosbeak	4	3.5

Although there are obvious discrepancies, the two sets of figures agree sufficiently to suggest that the strip-transect counts can be converted into densities with reasonable confidence. It is uncertain whether the strip method underestimates densities or whether the Wyoming figures are generally lower because of habitat differences.

TREATMENT OF DATA

The findings for each vegetation type are given in tables 2 to 7. Profiles (fig. 1) of three of the vegetation types are presented to show the foraging niches of the inhabiting birds. (I am indebted to Dr. T. I. Storer for suggesting this technique.) Nearly all the species considered in this report are shown.

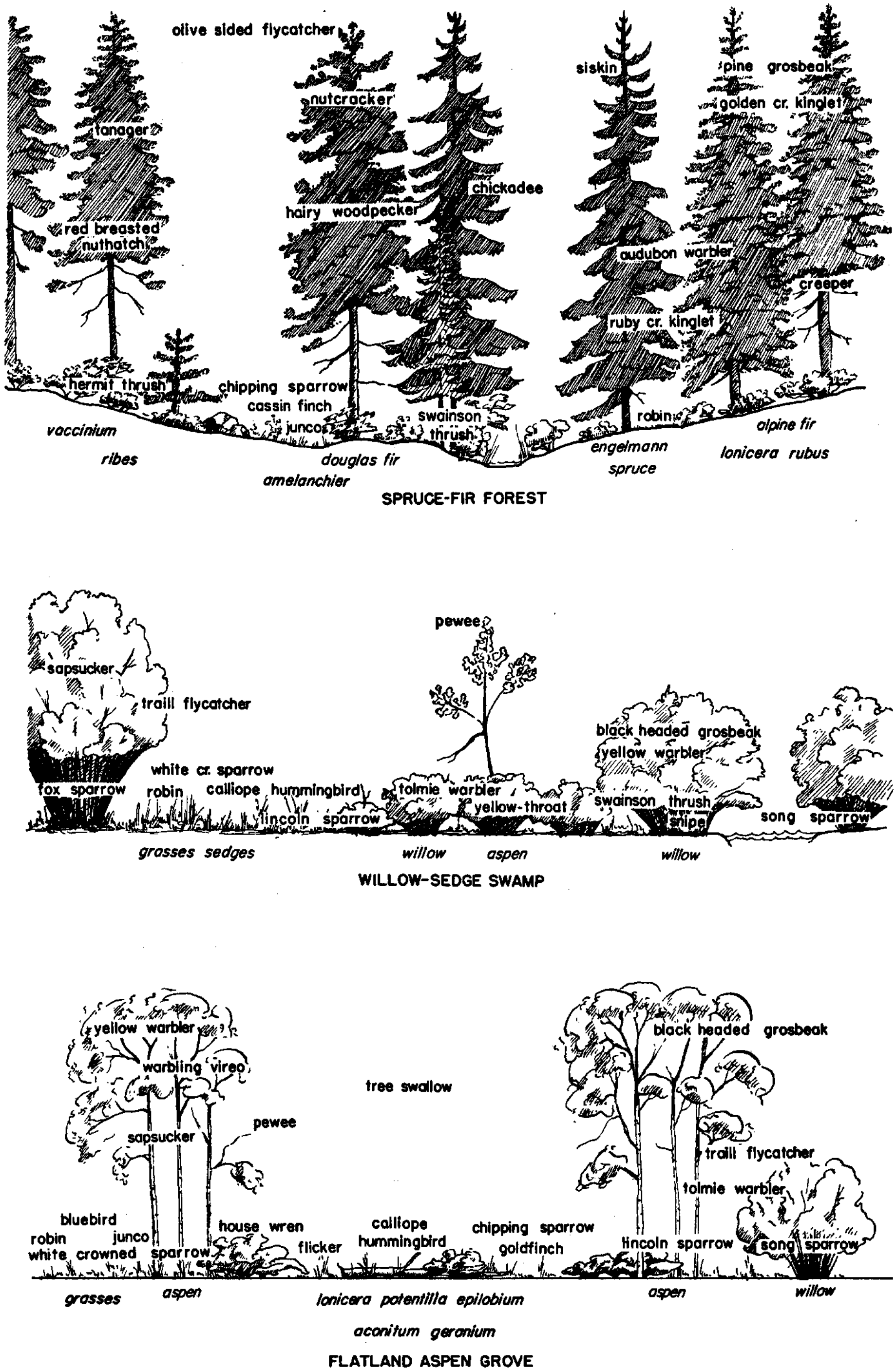

Fig. 1. Vegetation profiles showing foraging niches of the inhabiting species.

Census figures in the accompanying tables are given as mean numbers of individuals counted per trip. These are then converted to the standard value of birds per 100 acres. The species are listed in their feeding categories according to foraging level and food type as described in an earlier paper (Salt, 1953). One modification has been made; air feeders have been subdivided into soaring (A–S) and perching (A–P) categories. Other categories are: Foliage-nectar (F–N), Foliage-insect (F–I), Foliage-seed (F–S), Timber-searching (T–S), Timber-drilling (T–D), Ground-predator, (G–P), Ground-insect (G–I), and Ground-seed (G–S).

Turcek has inquired (letter) why I classified all species into either insect or seed eaters rather than using an additional category of mixed feeders as he has done. There is no doubt that these birds form an important group in any avifauna as he has shown. However, I wished to determine values for herbivore (primary consumer) and carnivore (secondary and tertiary consumer) biomasses (total weight of living material) and to do this each species must be placed in one or the other category. The mixed feeders were placed, then, according to which type of food formed the largest part of the diet.

At first thought it might be argued that food habits for the species should be determined for the area investigated. There can be no doubt that this would result in increased accuracy in classification of some species, especially if the further refinement were made of partitioning a biomass into categories according to the percentage of food of each type in the diet. However, a gram of insect material cannot be assumed to be necessarily equivalent to a gram of plant material or for that matter equivalent to dissimilar insect food. In view of this, there seems to be no great increase in accuracy possible without a simultaneous determination of caloric content of the food. I regard the latter procedure as highly desirable, but a program of food analysis of this magnitude could not be carried out at Jackson Hole.

If an avifauna is to be measured, some sort of unit must be used. Furthermore, the results must be expressed as multiples of that unit. The simplest characteristic to measure is the number of species making up the avifauna. If the generalization is accepted that each species occupies a unique niche, then the number of species gives an indication of ecologic diversity in the habitat. The total species composition of the seven avifaunas studied is shown in table 9.

Avifaunal composition is frequently expressed as numbers of individuals. I must admit that the value of this expression is not clear to me. It seems to imply that in some way three horned owls and one hummingbird are equal to four sparrows. What would seem to be a more meaningful measure is that given when these individual numbers are multiplied by the weight for each species. When this is done the results appear as one kind of biomass, standing crop biomass, that is, the biomass present at the time of census. These standing crop biomass figures indicate the total weight of the birds present on a unit area. Considering the matter from the point of view of community metabolism, they represent the total stored energy present as birds, or putting it another way, the amount of food available for things that eat birds. In the tables the total standing crop biomass is given for each feeding category.

A figure related to food consumption may be derived from the standing crop biomass by making use of a generalization from the field of bioenergetics. The conversion is made for each species by multiplying numbers of individuals times the mean weight of the species to the 0.7 exponent and then summing all the values for an avifauna or some part thereof. The resulting figures are referred to here as "consuming biomass." These can be taken as indicative of rate of food consumption or energy intake by the avifauna.

The reasoning in support of this method is as follows. Oxygen consumption per gram and hence calories consumed from one species or individual to another is known to be proportional to a mathematical derivative of body weight (Brody, 1945:352–374)—an exponential function. The precise value of this exponent has been a matter of some dispute; suggested values range from 0.62 to 0.73, but acting on advice from Dr. William R. Dawson, who is studying this subject, I have used 0.7. Even if the theoretically correct value proves to be somewhat different, using it would not improve significantly the accuracy of the figures given here.

When weights to the 0.7 power are used the lower metabolism per gram of large birds relative to small ones is cancelled out and all weights thus modified become equal in terms of caloric intake per gram under standard conditions at a given temperature.

It would be erroneous to argue that these values for consuming biomass could be converted to actual food consumption values in the wild if we only knew the correction factor to use, for two variables still remain uncorrected, environmental temperature and species differences in temperament. The major variable, temperature, actually introduces no great error for comparisons when the avifaunas considered have similar proportions of large and small species and are all in neighboring communities subject to the same macroclimatic regime. Under these circumstances the food consumption by all the avifaunas would experience parallel increases and decreases in response to temperature fluctuations and hence would remain comparable. One might argue that different species show different abilities to consume food at extreme temperatures, particularly cold. Dawson (1954), Salt (1952), Seibert (1949), and Kendeigh (1949) have shown, however, that species residing in a place having extreme weather are adapted to these conditions. The significant variable is, once again, size. If comparisons were to be made between avifaunas from significantly different climates, correction would undoubtedly be needed. That there are differences in temperament and activity rate between species is well known to all ornithologists. A phlegmatic vireo and an active warbler of the same weight certainly consume different amounts of food. Here, though, it seems probable the differences are small enough to be ignored for what are first approximations. On this basis, then, the "consuming biomass" figures are regarded as indices of food intake. They give no indication of absolute amounts of food required, but are useful for comparison. Two avifaunas may be regarded as consuming food at rates proportional to their respective consuming biomasses.

The weights used in the calculations are the means of samples in the Museum of Vertebrate Zoology collected nearest Jackson Hole. The birds are weighed when collected and the weight is recorded on the tag. It was not thought necessary to correct for sex and age distribution as suggested by Elton and Miller (1954). At the seasons when the censuses are made there are few birds present as immatures which are not recognizable as such. In addition, young birds rapidly reach adult weight after fledging. While there are differences between sexes, these were accounted for by averaging weights for both sexes and assuming an equal sex ratio.

For comparison with the results of the Wyoming study, biomass values have been calculated for avifaunas of three community successional series of the eastern United States: oak-hickory of the Georgia Piedmont (Johnston and Odum, 1956), beach-maple-hemlock of New York (Kendeigh, 1946), and beech-maple-pine of northern lower Michigan (Kendeigh, 1948). Weights for each species are taken from the literature for the locality nearest the area studied. Since in all of these reports densities of some birds are given as either plus or minus, a value of ½ bird per 100 acres was assigned to plus and ¼ to minus densities. The results of the calculations are given in table 10 and in figures 2 to 4. In the beech-maple-hemlock succession, biomass values have been calculated separately for the early, middle, and late facies of the avifauna of the mixed shrubs and small trees stage. In the Michigan report, data from two successional sequences are given; grassland-aspen-pine on the upland and cedar-aspen and cedar-balsam on the bogs. Both sequences lead to the same climax of beech-maple-pine. The two lines of succession are shown in the graph.

DESCRIPTION OF CENSUS AREAS

CONIFEROUS VEGETATION-TYPES

Lodgepole (table 2).—The lodgepole census area was at the northwest end of String Lake below the south shoulder of Indian Paintbrush Canyon at an elevation of 6900 feet. Near the lake the area is relatively flat but the slope becomes progressively greater

Table 2

Lodgepole Pine

(Distance, 0.49 miles; area, 10 acres; number of counts, 6)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Foliage-Insect					
Audubon Warbler (*Dendroica auduboni*)	0.67	6.7	13.1	88	41
Western Tanager (*Piranga ludoviciana*)	0.50	5.0	29.0	145	53
Totals				233	94
Foliage-Seed					
Canada Jay (*Perisoreus canadensis*)	0.30	3.0	74.6	224	62
Clark Nutcracker (*Nucifraga columbiana*)	0.17	1.7	130.0	221	51
Siskin (*Spinus pinus*)	0.17	1.7	12.1	1	10
Totals				466	123
Timber-Searching					
Mountain Chickadee (*Parus gambeli*)	0.67	6.7	12.0	80	38
Totals				80	38
Ground-Insect					
Chipping Sparrow (*Spizella passerina*)	0.17	1.7	12.2	21	10
Totals				21	10
Ground-Seed					
Oregon Junco (*Junco oreganus*)	1.00	10.0	17.7	177	75
Totals				177	75

toward the base of the mountain to the west. The canopy vegetation is an almost pure stand of even-aged lodgepole pines (*Pinus contorta*) forty to sixty feet high, spaced three to twelve feet apart. Only the top branches of the trees carry needles. Most of the space below this thin canopy is filled by scaffoldwork of bare trunks hung with dead branches. There are a few dead aspens (*Populus tremuloides*) standing in the forest and both fallen aspens and lodgepoles on the ground. The understory consists of scattered seedlings of alpine firs (*Abies lasiocarpa*) three to six feet high and a nearly continuous ground cover of *Lupinus* and grasses interrupted by *Lonicera* and *Vaccinium* bushes. There are a few large boulder outcrops, and the soil appears to be thin.

Lodgepole-spruce-fir (table 3).—This transect area was on the south shoulder of

Indian Paintbrush Canyon at an elevation of 7300 feet. The overstory vegetation is a mixture of three species; lodgepole pine, Engelmann spruce (*Picea engelmannii*), and alpine fir (*Abies lasiocarpa*); it is not, however, a uniform mixture. Rather, where the transect begins, lodgepole pine predominates with only a few spruce and fir present. Along the transect route spruces and firs gradually become more frequent so that where the transect ends they outnumbered the lodgepoles. Generally the trees are slender, 6 to 12 inches (d.b.h.) and closely spaced. To some degree the lodgepoles and generally the spruces and firs have some needles on the branches below the tops of the trees so that the canopy layer is thicker than in pure lodgepole forest. The understory is a somewhat sparse but continuous layer of shrubs—*Lonicera, Vaccinium, Ribes, Sorbus* and *Spirea*—except where rock outcrops exist or a windfall has made an opening in the forest. In these places grasses and smaller forbs such as *Lupinus* are more common. There are a

Table 3

Lodgepole-Spruce-Fir

(Distance, 0.85 miles; area, 15 acres; number of counts, 12)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Foliage-Insect					
Audubon Warbler (*Dendroica auduboni*)	2.75	18.3	13.1	240	112
Western Tanager (*Piranga ludoviciana*)	2.75	18.3	29.0	531	193
Ruby-crowned Kinglet (*Regulus calendula*)	1.42	9.4	6.1	57	33
Golden-crowned Kinglet (*Regulus satrapa*)	0.25	0.6	5.1	3	2
Totals				831	340
Foliage-Seed					
Clark Nutcracker (*Nucifraga columbiana*)	1.75	11.7	130.0	1521	351
Pine Grosbeak (*Pinicola enucleator*)	0.08	0.6	51.0	31	9
Totals				1552	360
Timber-Searching					
Mountain Chickadee (*Parus gambeli*)	1.17	7.8	12.0	94	44
Red-breasted Nuthatch (*Sitta canadensis*)	0.50	3.3	10.1	33	17
Creeper (*Certhia familiaris*)	0.08	1.1	8.0	9	5
Totals				136	66
Timber-Drilling					
Hairy Woodpecker (*Dendrocopos villosus*)	0.25	1.7	69.8	119	33
Totals				119	33
Ground-Insect					
Chipping Sparrow (*Spizella passerina*)	1.67	11.1	12.2	135	64
Robin (*Turdus migratorius*)	0.33	2.2	88.0	194	51
Totals				329	115
Ground-Seed					
Oregon Junco (*Junco oreganus*)	1.42	9.4	17.7	166	71
Cassin Finch (*Carpodacus cassinii*)	0.33	2.2	27.6	61	22
Totals				227	93

good many dead trees present; many are tangled with living trees and remain propped upright.

Spruce-fir (table 4; fig. 1).—The transect was made in a forest of Engelmann spruce and alpine fir containing some Douglas fir (*Pseudotsuga taxifolia*). It is on the south side of Indian Paintbrush Canyon near the mouth and at a slightly higher elevation,

Table 4

Spruce-Fir

(Distance, 0.7 miles; area, 13 acres; number of counts, 11)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Air-Perching					
Olive-sided Flycatcher (*Nuttallornis borealis*)	0.18	1.4	31.5	44	16
Totals				44	16
Foliage-Insect					
Audubon Warbler (*Dendroica auduboni*)	1.00	7.7	13.1	101	47
Western Tanager (*Piranga ludoviciana*)	1.73	13.3	29.0	386	140
Ruby-crowned Kinglet (*Regulus calendula*)	1.09	8.4	6.1	51	29
Golden-crowned Kinglet (*Regulus satrapa*)	1.54	11.9	5.1	61	37
Totals				599	253
Foliage-Seed					
Clark Nutcracker (*Nucifraga columbiana*)	2.64	20.3	130.0	2639	609
Pine Grosbeak (*Pinicola enucleator*)	0.45	3.5	51.0	179	55
Siskin (*Spinus pinus*)	0.18	1.4	12.1	17	8
Totals				2835	672
Timber-Searching					
Mountain Chickadee (*Parus gambeli*)	0.91	7.0	12.0	84	40
Creeper (*Certhia familiaris*)	0.55	4.2	8.0	34	18
Red-breasted Nuthatch (*Sitta canadensis*)	0.45	3.5	10.1	35	18
Totals				153	76
Timber-Drilling					
Hairy Woodpecker (*Dendrocopos villosus*)	0.36	2.8	69.8	195	55
Arctic Three-toed Woodpecker (*Picoides arcticus*)	0.09	0.7	73.2	51	14
Totals				246	69
Ground-Insect					
Robin (*Turdus migratorius*)	0.45	3.5	88.0	308	80
Chipping Sparrow (*Spizella passerina*)	0.36	2.8	12.2	34	16
Hermit Thrush (*Hylocichla guttata*)	0.45	3.5	25.6	90	34
Swainson Thrush (*Hylocichla ustulata*)	0.36	2.8	30.0	84	30
Totals				516	160
Ground-Seed					
Oregon Junco (*Junco oreganus*)	0.91	7.0	17.7	124	53
Cassin Finch (*Carpodacus cassinii*)	0.18	1.4	27.6	39	14
Totals				163	67

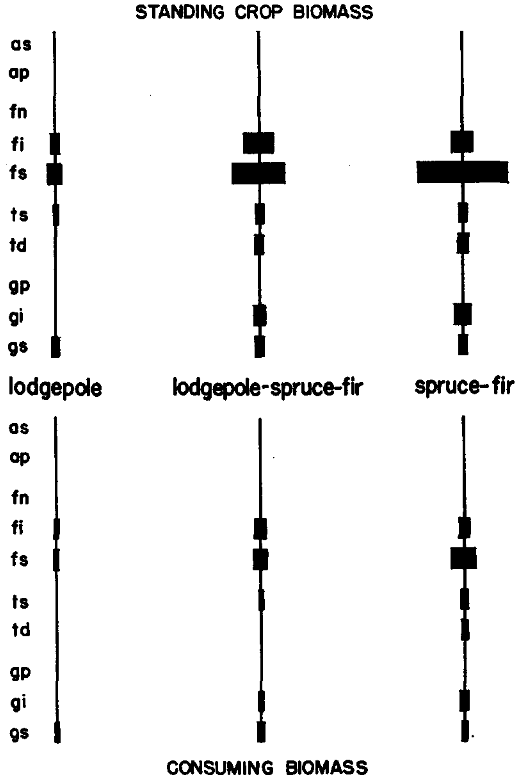

Fig. 2. Diagram of biomass values of the avifaunas of the three coniferous forest communities. The total length of each bar is proportional to the biomass in grams. For abbreviations, see table 8, and for actual biomass values, see tables 2, 3, and 4.

7600 feet, than the previous transect. The trees are large and mature, forming a semi-closed canopy sixty to one hundred feet from the ground. The canopy is locally interrupted by openings resulting from rock outcrops or windfalls. Moss grows on the tree trunks. The understory is a mixture of leafy shrubs: *Vaccinium, Lonicera, Rubus, Ribes* and *Amelanchier*. Seedlings of the dominant trees are also present. There is a fairly thick layer of duff over the ground in most places, and large boulders, some eight to ten feet in diameter, protrude through the understory. Several small streams cross the transect, and in one place the transect parallels the river of the canyon.

It seems reasonable to postulate that these three vegetation-types represent two successional stages plus an intermediate mixture of the series for this location. One is led to this view by seeing that alpine fir is replacing the lodgepole forest in transect 1. Furthermore, in transect 3 the Engelmann spruce, alpine fir and Douglas fir are all replacing themselves. All three communities stand on the same soil (Fryxell, 1930), namely glacial moraine composed chiefly of gneiss derived from parent material higher in the canyon itself.

DECIDUOUS VEGETATIONS

Willow-sedge swamp (table 5; fig. 1).—A floristic description of this vegetation is given by Reed (1952). The transect ran parallel to the dirt road between the Biologi-

Table 5

Willow-Sedge Swamp

(Distance, 0.5 miles; area, 10 acres; number of counts, 6)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Air-Perching					
Traill Flycatcher (*Empidonax traillii*)	5.17	51.7	12.7	657	305
Western Wood Pewee (*Contopus richardsonii*)	0.33	3.3	14.0	46	22
Totals				703	327
Foliage-Nectar					
Calliope Hummingbird (*Stellula calliope*)	4.33	43.3	2.5	108	82
Totals				108	82
Foliage-Insect					
Yellow Warbler (*Dendroica aestiva*)	10.17	101.7	9.7	986	498
Yellow-throat (*Geothlypis trichas*)	5.17	51.7	10.0	517	259
Tolmie Warbler (*Oporornis tolmiei*)	1.00	10.0	11.4	114	55
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.17	1.7	46.0	78	25
Totals				1695	837
Timber-Drilling					
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.67	6.7	45.2	303	96
Totals				303	96
Ground-Insect					
Robin (*Turdus migratorius*)	2.17	21.7	88.0	1910	499
Wilson Snipe (*Capella delicata*)	1.17	11.7	100.0	1170	294
Fox Sparrow (*Passerella iliaca*)	2.00	20.0	30.6	612	218
Lincoln Sparrow (*Melospiza lincolnii*)	6.50	65.0	17.5	1138	481
Swainson Thrush (*Hylocichla ustulata*)	0.67	6.7	30.0	201	72
Totals				5031	1564
Ground-Seed					
White-crowned Sparrow (*Zonotrichia leucophrys*)	1.50	15.0	28.5	428	156
Song Sparrow (*Melospiza melodia*)	3.00	30.0	21.0	630	252
Totals				1058	408

cal Station and the Jackson Lake Ranger Station on U. S. Highway 26 and 287. The Biological Station is 0.8 miles west of Moran at B.M. 6750. The vegetation consists of an irregular cover of low willows two to four feet high between which grow sedges and grasses. Within the low willow area are groves of large willows ten to twelve feet high. The groves are frequently "hollow" or circular with a stand of lush grass in the middle. Along the stream courses are willows six to ten feet high in a continuous cover. Moose trails criss-cross through the swamp as do the moose themselves at evening. During early summer the soil is saturated with water and forms a dark muck.

Scrub-meadow (table 6).—This transect was made in a mountainside area below

Table 6

Scrub-Meadow

(Distance, 0.1 miles; area, 2 acres; number of counts, 10)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Air-Perching					
Traill Flycatcher (*Empidonax traillii*)	0.2	10.0	12.7	127	59
Totals				127	59
Foliage-Nectar					
Broad-tailed Hummingbird (*Selasphorus platycercus*)	0.9	45.0	4.0	180	117
Totals				180	117
Foliage-Insect					
Warbling Vireo (*Vireo gilvus*)	1.2	60.0	11.3	678	330
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.9	45.0	46.0	2070	657
Tolmie Warbler (*Oporornis tolmiei*)	1.7	85.0	11.4	969	468
Yellow-throat (*Geothlypis trichas*)	0.1	5.0	10.0	50	25
Totals				3767	1480
Ground-Insect					
Swainson Thrush (*Hylocichla ustulata*)	1.0	50.0	30.0	1500	540
Lincoln Sparrow (*Melospiza lincolnii*)	1.0	50.0	17.5	875	370
Chipping Sparrow (*Spizella passerina*)	0.6	30.0	12.2	366	173
Robin (*Turdus migratorius*)	0.3	15.0	88.0	1320	345
Totals				4061	1428
Ground-Seed					
Oregon Junco (*Junco oreganus*)	0.7	35.0	17.7	620	263
Lazuli Bunting (*Passerina amoena*)	1.0	50.0	15.0	750	333
Song Sparrow (*Melospiza melodia*)	0.5	25.0	21.0	525	211
White-crowned Sparrow (*Zonotrichia leucophrys*)	0.7	35.0	28.5	998	364
Totals				2893	1171

Rockchuck Peak on the shoulder of Indian Paintbrush Canyon at an elevation of 7300 feet. The vegetation is the product of two principal influences: the small streams which run down the face of the peak through the region and keep the soil moist through the first half of the summer, and periodic avalanches in the winter and spring which subject the vegetation to repeated onslaughts. As a result the area is covered by a scrub of small aspens, some only two or three feet high and others five to ten feet high. All are bent downhill. Dominant with the aspens are shrubs such as *Ceanothus, Lonicera,* and *Prunus* and numerous forbs and grasses. In the moister portions are willow groves six feet high and larger aspens. Where there is a small level area the soil is deeper and a small grassy meadow is formed. Around the margins of the snowtrack, Engelmann spruce and alpine fir grow. Similar snowtrack scrub areas, frequently dominated by willows, are found throughout the canyons of the Tetons wherever the slope is too great to hold the snow-pack through the winter.

Flatland aspen (table 7; fig. 1).—The censuses were made in a series of contiguous aspen groves along the west bank of the "Snake-Knee" 0.6 miles east of the Biological Station. Each grove is a cluster, some "hollow," of aspens forty to seventy feet high. The center of the grove, if hollow, has many downed logs. The groves form a leafy open

Table 7

Flatland Aspen

(Distance, 0.3 miles; area, 6 acres; number of counts, 5)

Species by category	Mean number/ count	Number per 100 acres	Mean weight, grams	Standing crop biomass, grams per 100 acres	Consuming biomass, grams per 100 acres
Air-Soaring					
Tree Swallow (*Iridoprocne bicolor*)	28.0	467.6	20.0	9352	3787
Totals				9352	3787
Air-Perching					
Traill Flycatcher (*Empidonax traillii*)	2.6	43.4	12.7	551	256
Western Wood Pewee (*Contopus richardsonii*)	1.0	16.7	14.2	237	107
Totals				788	363
Foliage-Nectar					
Calliope Hummingbird (*Stellula calliope*)	0.8	13.4	2.5	34	25
Totals				34	25
Foliage-Insect					
Yellow Warbler (*Dendroica aestiva*)	7.6	126.9	9.7	1231	622
Tolmie Warbler (*Oporornis tolmiei*)	1.8	30.1	11.4	343	165
Black-headed Grosbeak (*Pheucticus melanocephalus*)	1.2	20.0	46.0	920	292
House Wren (*Troglodytes aedon*)	1.4	23.4	10.5	246	121
Warbling Vireo (*Vireo gilvus*)	0.8	13.4	11.3	151	73
Totals				2891	1273
Timber-Drilling					
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	3.0	50.1	45.2	2265	721
Totals				2265	721
Ground-Insect					
Flicker (*Colaptes cafer*)	3.2	53.4	145.0	7743	1736
Mountain Bluebird (*Sialia currucoides*)	1.8	30.1	26.6	801	299
Robin (*Turdus migratorius*)	1.8	30.1	88.0	2649	692
Lincoln Sparrow (*Melospiza lincolnii*)	3.2	53.4	17.5	935	395
Chipping Sparrow (*Spizella passerina*)	0.8	13.4	12.2	163	77
Totals				12291	3199
Ground-Seed					
White-crowned Sparrow (*Zonotrichia leucophrys*)	2.4	40.1	28.5	1143	418
Oregon Junco (*Junco oreganus*)	0.4	6.7	17.7	119	50
Song Sparrow (*Melospiza melodia*)	0.4	6.7	21.0	141	57
American Goldfinch (*Spinus tristis*)	0.4	6.7	12.0	80	38
Totals				1483	563

canopy. Below the canopy the ground is covered with a lush tangle of shrubs; *Epilobium, Potentilla, Geranium* and other shrubs as well as grasses and flowering herbs are present. Insects are abundant and the ground is usually moist.

Hillside aspen.—The transect in hillside aspens was made in a grove on the south-facing slope just north of Highway 26 and 287, 1.7 miles east of Jackson Lake Ranger Station. The elevation is about 6900 feet. In aspect it is a continuous stand of fairly closely spaced slender aspens twenty to forty feet high. The understory is a thick rank growth of shrubs and grasses with many fallen aspen trunks. Superficially these groves

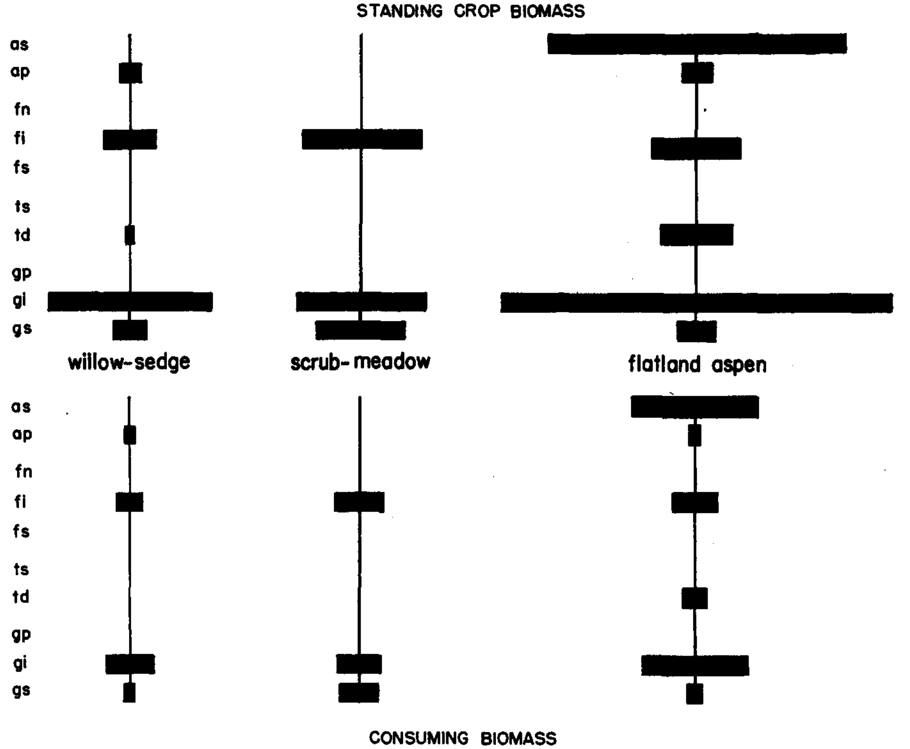

Fig. 3. Diagram of biomass values of the avifaunas of the three deciduous vegetation communities. For explanation, see figure 2. For actual biomass values, see tables 5, 6, and 7.

appear similar to those of the flatland aspen, but Reed's analysis demonstrates that there are fewer plant species composing the understory vegetation. No census data are given for this transect in the tables, but comments on the avifauna will be made in the discussion.

DISCUSSION

From the data in the tables and diagrams, certain inferences can be made about trophic or feeding relationships and community structure. However, before discussing these points it is important to call attention to the relationship between size of bird and required food intake. Large birds consume less oxygen and hence require less food per gram of body weight than small birds (Benedict, 1938; Brody, 1945). It follows that, from a community standpoint, a larger standing crop can be maintained on the same energy supply with large birds than with small ones. Also, large birds are not so sensitive to short term fluctuations in the food supply (Kendeigh, 1945). If two birds, alike in other respects, have ten per cent of their body weight present as stored food, a bird of 50 grams, for example, will last 1.6 times as long without food under a given set of conditions as a bird of 10 grams. Large size is not an unmixed blessing, however; a large bird eats more than a small one. Like all birds, they require that their food items be concentrated enough in location or present in large enough pieces so that they gain more energy from the food than they expend in gathering it.

Were the size-food requirement the only force operating, the avifauna would come to be entirely large birds. What brings about, then, the inclusion of small birds in an avifauna? It seems likely that natural selection acting on individuals of each species exerts a selection on the structure of the ecosystem to produce the most efficient utilization of the energy available under a given set of conditions (Allee, *et al.,* 1949: 695–729). Under this selective pressure no energy source remains unexploited for long. Much of the energy of the community is trapped in small particles of matter such as seeds, egg masses of spiders, scale insects and the like. Since only a small bird having specialized feeding apparatus and habits can gather these small particles efficiently, the avifauna comes to be composed of birds of a variety of sizes corresponding to the feeding niches available. But within each feeding niche the advantage of larger size still operates, and it would appear that each species tends toward the largest size that its feeding procedures will permit.

These relationships play an important role in determining avifaunal structure of a community as will be illustrated in the remarks which follow.

The three coniferous forest types, for reasons already given, I regard as successional stages in a series, lodgepole pine being earliest and spruce-fir latest. It is apparent when one walks through these three forests that from the lodgepole to the spruce-fir there is a progressive increase in green leaf surface. The canopy in the spruce-fir forest is thicker and more nearly complete and the forest floor is in darker shade. At the same time the plant understory is more complete than in the lodgepole forests. It seems evident that the spruce-fir forest is trapping a larger amount of solar energy and that the flow of energy through the community is therefore greater than through the lodgepole forest.

In the avifaunas of these forests parallel differences exist as can be seen in the tables and diagram. As succession proceeds from the lodgepole stage to the spruce-fir stage, the number of species of birds in the avifauna increases. A similar increase has been found in other successions (Kendeigh, 1946, 1948; Odum, 1950; Johnston and Odum, 1956). Moreover, the increase is not an increase in the number of species feeding in the canopy and a decrease in the birds feeding on the ground but an increase in all categories. These changes may be interpreted as reflecting the increase in complexity of the vegetation. The changes suggest that in early seral stages only sufficient food energy is present in a given stratum or feeding category to support a few generalized species. As the community matures, enough energy flows through the stratum so that it may be partitioned between a number of specialized species. When this happens, one may presume that the generalized species, if they are to remain in the avifauna, are forced by competition to adopt more specialized feeding habits themselves.

Not only does the number of species increase but the biomass values also increase from early to late successional stage. Standing crop biomass increases by over four times and consuming biomass by nearly that much.

There is a change in the ratio of consuming biomass to standing crop biomass from early to later successional stage (table 8). In the lodgepole avifauna it is 0.35, in the lodgepole-spruce-fir 0.32, and in the spruce-fir 0.29, a progressive and regular decrease in this ratio. This means that there is a progressive increase in the percentage of the bio-

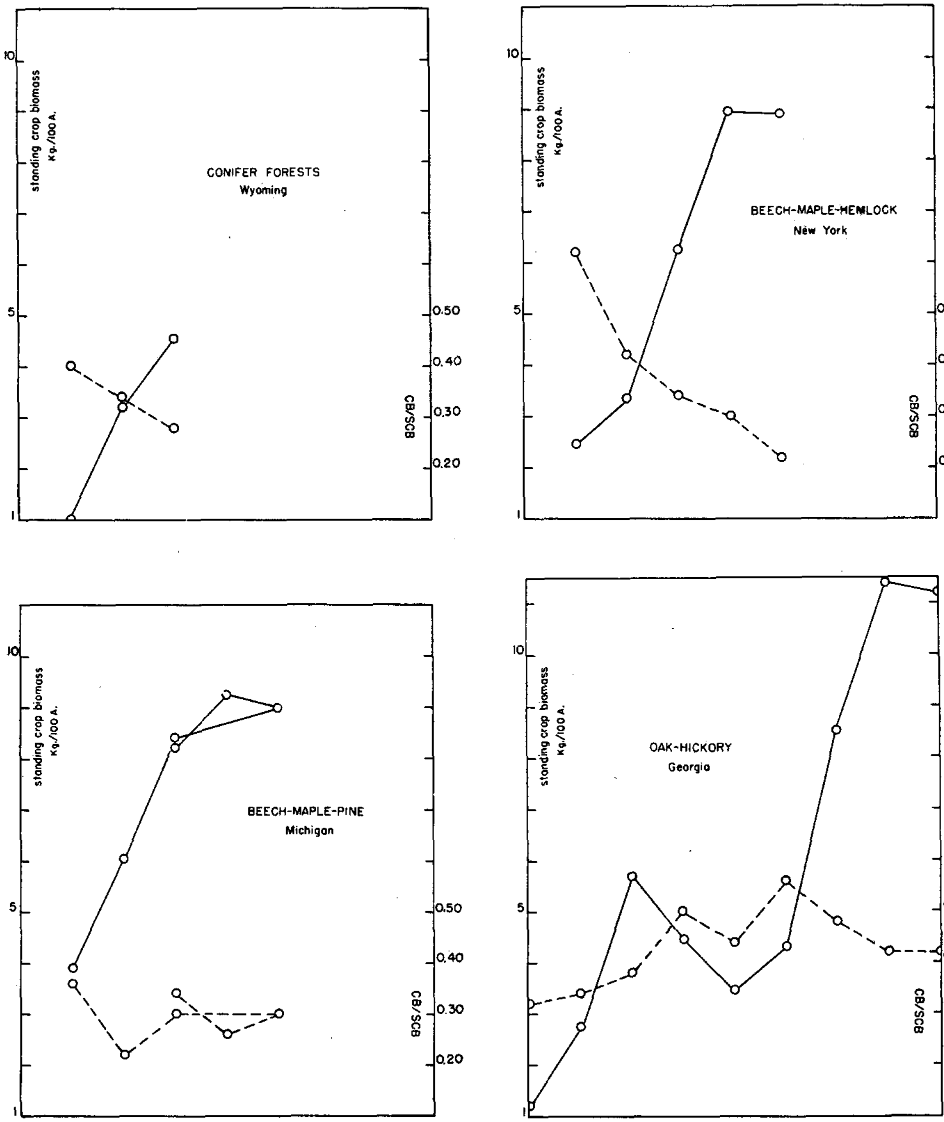

Fig. 4. Graphs of avian standing crop biomasses (solid line) and consuming biomass-standing crop biomass ratios (broken line) in stages of the Wyoming coniferous forest, beech-maple-hemlock, beech-maple-pine, and oak-hickory successions. Stages of each succession are plotted as abcissae.

mass of the avifauna present as larger species. Applying the generalizations discussed above, it becomes evident that the later successional stage is supporting a larger biomass on a given energy budget than is the earlier stage. The avifauna of spruce-fir community then can be said to have not only a greater energy flow through it but a greater efficiency in utilizing this energy.

Censuses of birds are known to have high variances regardless of the methods employed (Dice, 1952:76–78), so it is well to be cautious in generalizing from such data.

Table 8

Biomass Values per 100 Acres, and Ratios

	Standing crop biomass, grams	Consuming biomass, grams	Ratio
Lodgepole pine, table 2			
Primary consumers G-S, F-S	643	198	
Secondary consumers G-I, T-S, F-I	334	142	
Totals and ratio	977	340	0.35
Lodgepole-spruce-fir, table 3			
Primary consumers G-S, F-S	1779	453	
Secondary consumers G-I, T-D, T-S, F-I	1415	554	
Totals and ratio	3194	1007	0.32
Spruce-fir, table 4			
Primary consumers G-S, F-S	2998	739	
Secondary consumers G-I, T-S, T-D, F-I, A-P	1558	574	
Totals and ratio	4556	1313	0.29
Willow-sedge swamp, table 5			
Primary consumers G-S, T-D, F-N	1469	586	
Secondary consumers G-I, F-I, A-P	7429	2728	
Totals and ratio	8898	3314	0.37
Scrub-meadow, table 6			
Primary consumers G-S, F-N	3073	1288	
Secondary consumers G-I, F-I, A-P	7955	2967	
Totals and ratio	11028	4255	0.39
Flatland aspen, table 7			
Primary consumers G-S, T-D, F-N	3782	1309	
Secondary consumers G-I, F-I, A-P, A-S	25322	8622	
Totals and ratio	29104	9931	0.34

Abbreviations: A-S, air-soaring; A-P, air-perching; F-N, foliage-nectar; F-I, foliage-insect; F-S, foliage-seed; T-S, timber-searching; T-D, timber-drilling; G-I, ground-insect; G-S, ground-seed.

But two of the graphs, that of the beech-maple-hemlock of New York and the beech-maple-pine of Michigan show the same consistent increase in standing crop biomass from early to late stage as is shown by the Wyoming graph, and the graph of the oak-hickory of Georgia shows the same general trend with a sharp dip in the middle. Whatever the interpretation of the entire trend of the Georgia graph, the trend in the latter half of the succession is consistently upward. It seems quite reasonable to conclude, then, that we may expect to find in a great many successions an increase in standing crop biomass from early to late seral stages. This parallels the increases in numbers of species of birds and of individuals which we have come to expect from earlier studies.

The trend in the value of the ratio of consuming biomass to standing crop biomass is really of more fundamental import than the standing crop biomass. Remembering that the efficiency in energy utilization of the avifauna of a community is concluded to

Table 9

Numbers of Species

	Vegetation-type					
Feeding category	Lodge-pole	Lodgepole-spruce-fir	Spruce-fir	Willow-sedge	Scrub-meadow	Flatland aspen
Air-Soaring	....	....	....	....	....	1
Air-Perching	....	....	1	2	1	2
Foliage-Nectar	....	....	....	1	1	1
Foliage-Insect	2	4	4	4	4	5
Foliage-Seed	3	2	3	....	....	....
Timber-Searching	1	3	3	....	....	....
Timber-Drilling	....	1	2	1	....	1
Ground-Insect	1	2	4	5	4	5
Ground-Seed	1	2	2	2	4	4
Totals	8	14	19	15	14	19

be inversely proportional to this value, a declining value or slope should be read as indicating an increase in efficiency. We have already noted that such an increase in efficiency can be seen in the Wyoming coniferous succession. In the successions from the eastern United States a similar increase in efficiency can be seen clearly in the beech-maple-hemlock of New York, an initial high efficiency followed by a decline and then a rise in efficiency in the later stages in the Georgia succession and an irregular pattern of values in the succession in Michigan which might possibly be interpreted as showing a slight overall increase in efficiency, although it does very little to support a generalization one way or another.

From the graphs it is possible to say that frequently succession in avifaunas will show an increase in efficiency with seral progression, the avifauna of the climax community being the most efficient in energy utilization.

Parenthetically, an illustration of the value of this type of study in community ecology may be inserted. While I was in Wyoming I heard plant ecologists debating whether the alpine fir-Engelmann spruce forest was the climax vegetation of the Teton canyons or not. Now, it will be noticed that in the graphs of the eastern successions the subclimax has a standing crop biomass that is nearly as great as or is greater than that of the climax. By analogy then, one might argue that the spruce-fir is probably not the climax but the subclimax. The climax is perhaps some other community which has been removed either by lumbering or fire, possibly Douglas fir, as some botanists believe.

It will be noticed that in the avifaunas of the coniferous forests the biomass of primary consumers or herbivores exceeds that of the secondary consumers or carnivores while in the deciduous forest avifaunas just the reverse relationship exists. This would seem to be a significant and fundamental difference between these two types of avifaunas. However, no such relationship seems to exist in the examples from the eastern United States, so there is no way of assessing the importance of this observation until more information from other areas becomes available.

The three deciduous vegetation communities do not stand in any relationship to one another in succession. They are in fact very likely to be members of different successional series. The flatland aspen and willow-sedge swamp communities are both on soil the parent material of which is outwash or till from Pinedale glaciers from the north. The principal constituent is quartzite, whereas the scrub-meadow community is on the same gneiss-dominated moraine soil as are the coniferous forest communities. All three communities have high ground moisture, especially the swamp which is covered with water during the early summer. In spite of these differences, the structures of the vegetation of the willow-sedge swamp and the mountainside scrub-meadow communities are very similar. Although the numbers of species in the two avifaunas are nearly the same, the willow-sedge swamp avifauna shows slightly more diversity into different niches and a lower ratio of consumer biomass to standing crop biomass and hence higher efficiency.

Table 10

Avifaunal Characteristics of Three Successions of the Eastern United States*

Beech-maple-hemlock, New York (Kendeigh, 1946)

	Mixed shrubs and small trees: Early	Middle	Late	Hemlock-beech	Beech-maple-hemlock
Standing crop biomass, gms.	2451*	3347	6255	8967	8902
**CB/SCB ratio	0.46	0.36	0.32	0.30	0.26

Beech-maple-pine, Michigan (Kendeigh, 1948)

	Grass-land	Aspen-red maple	Pine-aspen	Cedar-aspen	Cedar-balsam	Beech-maple-pine
Standing crop biomass, gms.	3930	6038	8405	8238	9249	8989
CB/SCB ratio	0.33	0.26	0.30	0.32	0.28	0.30

Oak-hickory, Georgia (Johnston and Odum, 1956)

	Grass-forb 1	Grass-forb 2	Grass-shrub 1	Grass-shrub 2	Pine forest 1	Pine forest 2	Pine forest 3	Pine forest 4	Oak-hickory
Standing crop biomass, gms.	1210	2742	5703	4453	3460	4317	6582	11419	11215
CB/SCB ratio	0.31	0.32	0.34	0.40	0.37	0.43	0.39	0.36	0.36

* Quantities expressed on basis of 100 acres for each community.
** Consumer biomass-standing crop biomass ratio.

The standing crop biomass for the flatland aspen avifauna is certainly too large. Many of the birds in those groves, such as robins and flickers, do a considerable part of their feeding outside the groves. It is impossible to estimate what percentage of their energy comes from outside the groves, but even if the value for the standing crop biomass for the whole avifauna were cut in half, it would still be a figure comparable in size with those for the two other deciduous-vegetation communities.

We may compare this figure with that of the hillside aspen groves. It was mentioned earlier that these groves appear superficially similar to some of the flatland groves, and one might infer that many of the same niches should be present. These hillside groves, because of soil characteristics and slope are drier than the flatland groves. Furthermore, the two types "differ markedly from a floristic point of view" (Reed, 1952:710). The hillside community shows a much less varied flora than that of the flatland, having only about half the number of shrubs, forbs, and grasses. It seems likely that the metabolic efficiency of the hillside groves is also less than that of the flatlands, although it would not be obvious from their appearance. Significantly the avifauna also is impoverished, in fact more markedly than the flora. I found the following species established in the hillside grove: Warbling Vireo, Lazuli Bunting, Black-headed Grosbeak, Western Tanager, Audubon Warbler (doubtful), Yellow-bellied Sapsucker, and Western Wood Pewee. In counts on a transect of the same size as that in the flatland aspen the maximum number of individuals found of all species combined was fourteen; more often it was five to ten. When compared with the flatland groves, the difference is impressive. The avifaunas appear not only to respond in the same way as the plants to the two sets of conditions, but in an even more extreme manner.

It now remains to combine all the relationships discussed into a unified statement regarding avifaunas and their place in the communities of which they form a part. The community in the sense of an ecosystem undergoes a series of integrated changes as succession proceeds toward the climax. The avifaunal constituent of the community participates in these changes in a regular and apparently predictable pattern. This pattern consists of the following increases: numbers of species, reflecting an increase in diversity of habitat; numbers of individuals; standing crop biomass; and, in the latter stages of the succession, greater efficiency and stability of the avifauna judged by its utilization of the energy resources of the community. The highest standing crop biomass occurs in either the subclimax or climax. The energy flow through the avifauna, as indicated by consuming biomass, increases from early to later stages.

The avifauna is a constituent of the community integrated with the rest of the ecosystem in development during succession. The question now arises as to how close this integration is. Does the avifauna parallel precisely or nearly precisely the development in energy utilization of the entire ecosystem? If it does, then a measure of the energy metabolism of the avifauna will provide an index of the metabolism of the entire community to be used for comparisons between stages in the succession and between ecosystems. There is not nearly enough information available now to form a basis for an answer to this question. Palmgren (1928) found that in the avifaunas of the forests of Finland the number of birds was greater in the more productive forest-types. In Wyoming, the consuming biomass of the avifaunas increases with community succession in the coniferous forests and parallels soil and vegetation characteristics in the aspen groves. All of these circumstances suggest that a relationship probably exists between avifaunal biomass and community energy utilization.

SUMMARY

Censuses by strip transect of bird populations in six vegetation types at Jackson Hole, Wyoming, have been made. The three coniferous vegetation types are lodgepole, lodgepole-spruce-fir, and spruce-fir. These three are regarded as a successional sequence. The three deciduous forest types are willow-sedge swamp, scrub-meadow, and flatland aspen.

The avifauna of each community has been analyzed into categories on the basis of feeding habits. Standing crop biomasses (total weight of living material) for each category and avifauna have been calculated. A consuming biomass of an avifauna is defined as the sum of species consuming biomasses. These are calculated by multiplying number of individuals times the mean weight of the species to the 0.7 exponent. Grams of consuming biomass are regarded as equivalent in terms of food consumption regardless of size of species. Total consuming biomass is taken as an index to energy metabolism by an avifauna. The efficiency of a species in energy use is proportional to its size. As a product of this relationship, the efficiency of an avifauna is indicated by the proportion

of its biomass made up of large birds. This value is measured by the ratio of consuming biomass to standing crop biomass. The smaller the value, the greater is the efficiency.

In the coniferous forest avifaunas an increase has been found in standing crop biomass and in efficiency, as measured by the ratio of consuming biomass to standing crop biomass, as succession proceeds toward the climax. Similar relationships have been found in the avifaunas of three successions of the eastern United States reported in the literature: oak-hickory of Georgia, beech-maple-hemlock of New York, and beech-maple-pine of Michigan.

In the avifaunas of Jackson Hole those of the coniferous forest have a greater herbivore (primary consumer) biomass than they do carnivore (secondary and tertiary consumer) biomass. In the deciduous forest avifaunas the relationship is reversed.

Willow-sedge swamp and scrub-meadow avifaunas of Jackson Hole are of about equal standing crop biomass, but that of the willow-sedge swamp is more diversified, having more species in more categories.

The avifaunas of the aspen groves parallel in a magnified way, in their species composition and biomasses, differences in floristics of hillside aspen and flatland aspen groves. Hillside aspen groves, which have about half the number of species of plants present in flatland groves, also have a meager avifauna. The avifauna of the flatland groves is rich and varied and has a large standing crop biomass.

It is suggested that avifaunal size and efficiency in energy metabolism may prove to reflect ecosystem functions accurately enough so that avifaunal characteristics may be used as indices of the metabolism and efficiency of the entire biotic community.

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