BIRD POPULATIONS OF ASPEN FORESTS IN WESTERN NORTH AMERICA

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ORNITHOLOGICAL MONOGRAPHS NO. 19
PUBLISHED BY
THE AMERICAN ORNITHOLOGISTS' UNION
1976

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ORNITHOLOGICAL MONOGRAPHS

This series, published by the American Ornithologists' Union, has been established for major papers too long for inclusion in the Union's journal, *The Auk.* Publication has been made possible through the generosity of Mrs. Carll Tucker and the Marcia Brady Tucker Foundation, Inc.

Correspondence concerning manuscripts for publication in the series should be addressed to the Editor, Dr. John William Hardy, Department of Natural Science, The Florida State Museum, University of Florida, Gainesville, Florida 32611.

Copies of *Ornithological Monographs* may be ordered from the Assistant to the Treasurer of the AOU, Glen E. Woolfenden, Department of Biology, University of South Florida, Tampa, Florida 33620. (See price list on back and inside back cover.)

Ornithological Monographs, No. 19, viii + 97 pp.

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First received, July 1970; accepted, September 1971; final revision completed, July 1975

Issued January 30, 1976

Price $7.50 prepaid ($6.00 to AOU Members)

Library of Congress Catalogue Card Number 75-46439

Printed by the Allen Press, Inc., Lawrence, Kansas 66044

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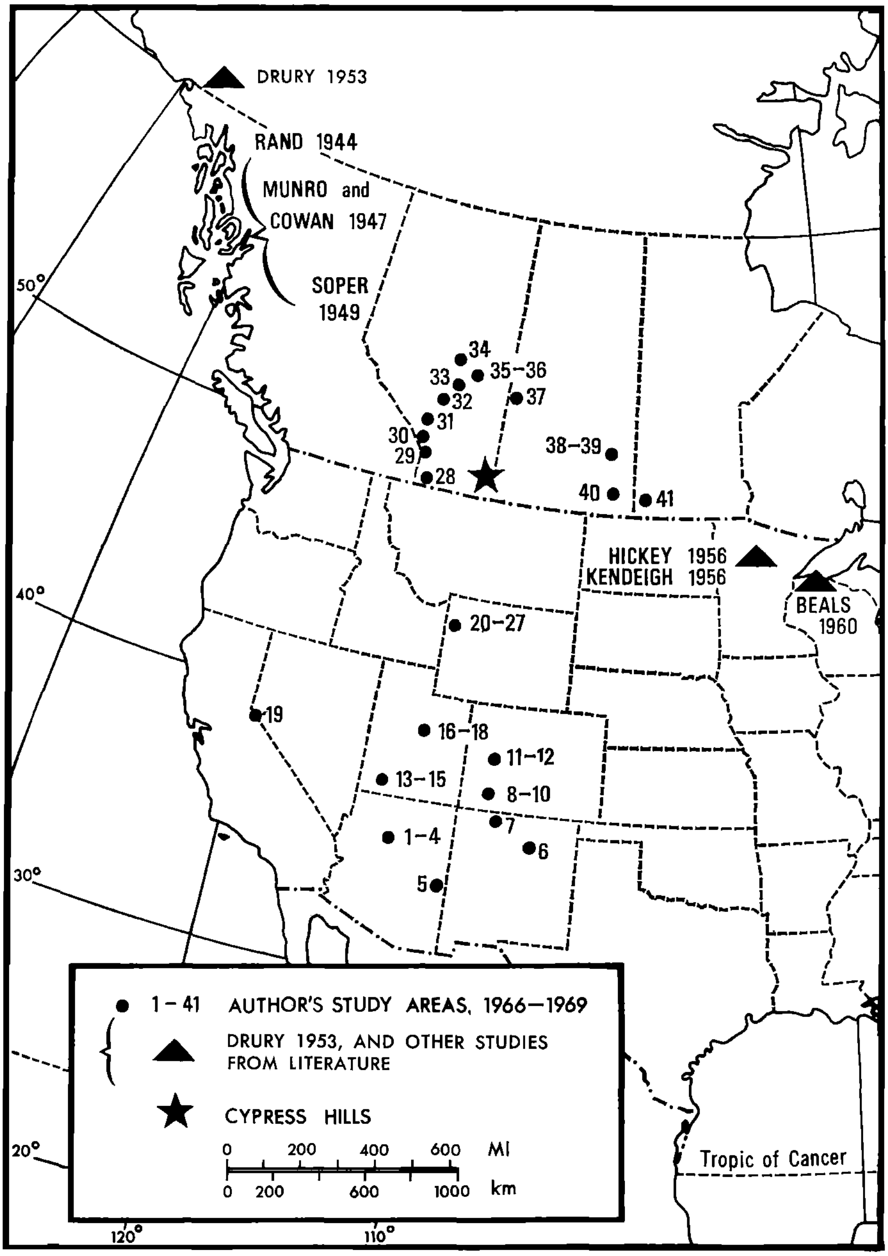


Aspen forest study areas mentioned in text.

TABLE OF CONTENTS

LIST OF FIGURES

TABLES

INTRODUCTION

The patterning of populations of plants and animals is probably the result of selection over time of organisms according to their individual physiological tolerances, behavioral adaptations to an environmental complex, and geographical availability (Gleason 1926). In certain situations a single factor, often floral, exhibits a controlling influence on the aggregation of organisms (Curtis 1959). Dominant organisms such as aspen trees influence immediate environmental conditions in a way which tends to sort the species aggregations according to the characteristics of the dominant. The relations between the aggregations, however, are generally continuous (Bray and Curtis 1957; Bond 1957; Beals 1960), but the limitation of some major feature of the environment, or of the aggregation of plant species such as by physiognomy, or species composition enables the ecologist to define a unit for analysis.

Aspen (*Populus tremuloides*) often occurs in essentially pure stands at mid-altitudes throughout a large region of the western mountains of the United States, and at lower elevations in the Canadian parkland and mixed boreal forest. The physiognomy of these forests is everywhere similar but differs from the coniferous forests, meadow, and prairie with which aspen forests are closely associated. I have arbitrarily chosen the sharp physiognomic boundary created by this dominant deciduous species to define the limits of a community that on the basis of understory plant species composition, is not always so discrete (Lynch 1955; Langenheim 1962).

Practically all of the quantitative analyses of bird populations in western North America have been restricted to local areas and the habitats studied have not often been described quantitatively. Regional studies have been descriptive in nature. As a result, the ecological relationships of bird populations of the major forest types throughout their entire range are not well known.

Therefore, the immediate objective of this study is to analyze quantitatively and to compare systematically the species composition and density of breeding bird populations as they are related to the distribution and structure of monotypic aspen forests in the two areas: a) from Arizona to northern Wyoming, and b) from southwestern Alberta to Manitoba.

Quantitative data of this nature are relevant to five problems to which this study is specifically applied: 1. the nature of community organization; 2. factors in forest structure which determine habitat selection; 3. ecological specialization and equivalence in animal communities; 4. relations of forest structure and latitude to diversity in bird populations; 5. the historical and geographical origin of the birds of aspen forests in relation to the establishment of *Populus tremuloides* in the western mountains and northern prairies.

The Nature and Choice of Study Areas

Throughout most of its extensive range, aspen is a pioneer species that is replaced rather quickly by longer lived, more shade tolerant species (Baker 1925; Fowells 1965). The clonal root systems are more permanent than above ground stems (Barnes 1966). Yet in the central Rocky Mountain region the species apparently maintains itself in extensive pure stands for centuries (Fetherolf 1917; Baker 1918, 1921, 1925; Reed 1952; Marr 1961; Langenheim 1962; Ream 1963). The distribution of these forests is disjunct, the populations being separated by great distances and topographic barriers of considerable significance. The largest pure stands are found in Utah and western Colorado where they are often the most important forest type. Large stands of aspen are absent from most of Montana.

Just south of Canada and east of the Front Range, the parkland aspen of the prairie-forest ecotone begins and extends in a continuous arc of variable width north into Alberta and Saskatchewan and south into Manitoba. Here also the species maintains itself in extensive pure stands for centuries (Bird 1930, 1961; Moss 1955; Lynch 1955). In this region the poplars *Populus trichocarpa* and *P. balsamifera* are sometimes a minor component. North of the parkland region and extending west into Alaska, the dominant species over millions of acres of the mixed boreal forest are aspen and balsam poplar.

Aspen is clonal in nature (Gifford 1966; Barnes 1966), and the extensive root systems give rise to dense, even-aged forests following removal of the canopy by some sudden disturbance. As a stand matures the density of the stems drops, while height, size of crown, and diameter of bole increases. Beyond maturity, the canopy begins to open up, making it possible for suppressed saplings to fill in the gaps. I have found that at this stage two lines of development are possible. The stand can either develop into a many-aged forest, or in the Rocky Mountains it can continue to open up, with little or no successful reproduction, until there are essentially no mature trees standing. The former trend seems to be the more usual; the factors causing the second are not understood, but heavy use in winter by elk in some regions and by cattle and sheep in summer in others, microclimatic changes due to loss of canopy and regional climatic changes are probably important influences.

A typical mature aspen stand is composed of straight tall trees pruned of dead branches to within at least ten feet of the bottom of the crown. Tree crowns frequently are not touching and are not dense with foliage but are similar in height. Understory trees are sometimes present. Shrub cover in the Rocky Mountains varies from being moderate to absent, while ground cover is composed of varying amounts of grasses, sedges, and forbs. The general appearance is one of openness. In Canada some forests have an exceedingly dense shrub cover.

The important plant communities found in association with aspen in Arizona and New Mexico are those dominated by Engelmann Spruce (*Picea engelmannii*) and firs (*Abies* spp.), Ponderosa Pine (*Pinus ponderosa*) and grasses and forbs. In western Colorado and Utah, spruce-fir forests, sagebrush (*Artemisia* spp.) and meadows are in close association, while in western Wyoming and southeastern Idaho, forests of Lodgepole pine (*Pinus contorta*), Engelmann Spruce, and cottonwood (*Populus angustifolia* and *P. balsamifera*); and willow (*Salix* spp.) and sagebrush (*Artemisia* spp.) flats; and meadows of sedges, grasses and forbs are important surrounding vegetation types. In California, sagebrush and meadow were associated with aspen stands studied. In Canada, grasslands interdigitate with aspen on one side and mixed boreal forest on the other. More complete discussions may be found in Reed (1952), Beetle (1961), Langenheim (1962), Ream (1963) and Fowells (1965) for the western mountains, and Lynch (1955), Moss (1955) and Bird (1961) and Rowe (1959) for the parkland.

Study areas were located in the San Francisco Mountains (1–4) and White Mountains (5) of Arizona at elevations of 8,000 to 10,000 feet, and the Sangre de Cristo Range (6) and San Antone Peak (7) of New Mexico at 9,800 and 10,000 feet; the Telluride Mountains of southwestern Colorado (8–10) at 9,000 feet, the area of Gothic, and Kebbler Pass Colorado (11–12) at 9,500 and 9,000 feet; at 9,000 feet on Webster flat (13–15) in southern Utah, at 8,000 feet on the Wasatch Plateau of central Utah (16–18); at 8,000 feet on Monitor Pass (19) in east central California, and at 6,000 to 6,800 feet in Jackson Hole, Wyoming (20–27). In Canada study areas were located in southwestern Alberta at 4,200 feet (28–29), in central Alberta at 3,800 to 2,000 feet (30–36), in Saskatchewan at 2,800 to 1,600 feet (37–40) and in Manitoba at 1,500 feet (41). Stands 28–30 were located in the narrow band of aspen parkland in the foothills (see Lynch 1955), while stands 31–33 and 35–36 were located in the ill-defined region between parkland and aspen poplar woodland (see Bird 1961, Rowe 1959 and the Atlas of Alberta 1969). Stands 37–41 were within the more eastern parts of the parkland. Stand 34 was located well within the mixed boreal forest region and is therefore treated separately. The frontispiece shows these locations in relation to some other descriptions of bird populations in aspen forests.

METHODS

Data were collected from relatively homogeneous stands for tree size and distribution. They measured 900 × 900 feet and were located within pure (or almost pure) aspen forests ranging from 30 to many thousands of acres in extent. In some of the stands widely scattered conifers were found in the understory and occasionally in the overstory. Most stands outside of Arizona were isolated from coniferous forest by no less than several hundred yards of aspen, meadow, or sagebrush. Forests with an extremely dense shrub cover, typically of hazel (*Corylus cornuta*) in Canada, were avoided because of the great difficulty in censusing their birds.

In order that variability between stands and between regions could be more thoroughly sampled, as many stands as possible were studied. Therefore, rapid techniques for sampling bird populations and vegetation were used.

Four parallel transects 300 yards long and spaced 225 feet apart were marked out with colored plastic flagging in each stand during the spring of 1968 and 1969. The use of a compass was necessary in order to accomplish this accurately and rapidly. The lines served to guide strip surveys of the birds.

Stands 20–27 were sampled in the spring and summer of 1966 using slightly different methods. The 1200 yard strip survey was bent around within a stand. Stand 19, in California, was atypical since data from two blocks of rather irregular shape, separated by 50 yards of sagebrush, were combined to form one stand. Stand 38, in Saskatchewan, was large enough for only one-half (600 yards) of a transect, but was used because it was the only stand of high tree density that could be located.

Ten sets of three circular quadrats marked with a tape around a center stake were used to sample trees, saplings and shrubs during 1966 (20–27). These were located using a grid and table of random numbers. The diameter at breast height (dbh) of each tree (greater than 1″) and height to top and bottom of the crown of four trees (measured with an inclinometer and range finder) were recorded in ⅒ acre circular quadrats. Within that quadrat a fortieth acre (18′6″ radius) quadrat was used and the height of each sapling was measured. A quadrat of 1/100 acre (11′7″ radius) was used to estimate, with a tape measure, height and percent cover of shrubs.

In 1968 and 1969 for stands 1–19 and 28–41 twenty fortieth acre quadrats were evenly spaced along the length of the four marked, parallel lines. The above data on vegetation were recorded.

A periscope tube with a plumb, grid, and calibrated diaphragm was used to estimate percent cover of the canopy. Eighty readings were evenly spaced along parallel lines in all stands. Each reading estimated the percent of the sky obscured by the vegetation overhead. A similar instrument has been described by Emlen (1967) for taking point samples of the overstory.

Ground cover was estimated using 40 quadrats, one yard square, spaced evenly along parallel lines in all stands. Percent cover of litter, bare earth, grasses, forbs, and average and maximum height of herbaceous vegetation were estimated in each. Species present in each quadrat were noted. Since no more than one day was spent sampling vegetation (June–July) in any one stand (except 20–27), identification of all understory species was not possible.

Objective samples of this nature give rapidly obtained relatively accurate summary data for many structural parameters in a stand and are useful for comparisons between stands. Statistical treatment of within-stand parameter variation is not justifiable (except in 20–27) because the sampling method was not random.

A strip survey method of estimating relative abundance of bird populations was used, recording birds detected within 75 ft of either side of a transect route followed in a standard manner. After the observer stood silently for several minutes, he walked slowly for 100 yards, and stood for several more minutes. This was repeated twelve times for a total coverage of a strip 1200 yards in length and 150 feet in width (12.4 acres). The data are used for comparison of abundance of species and total populations between stands.

It took between 1.5 and 2 hours to survey one stand and, since the stands were spread out and the census usually carried out only between sunrise and midmorning, a maximum of two stands could be sampled a day.

During 1966 (20–27), the strip looped back and forth within a stand in variable patterns that did not cross or overlap. In all other stands, the strip followed carefully marked out parallel center lines. Four surveys were made in stands 20–27 and two surveys in all other stands.

The relatively easily registered singing male was the unit recorded for passerines. Swallows were recorded when seen flying or perched in or near a hole. Hummingbirds were recorded as they flew as were species with large territories such as owls, hawks and ravens. Recorded single woodpeckers were counted as pairs if they appeared in two counts, the pair was seen, or the nest was found. The discovery of nests confirmed the breeding status of most species.

The maximum population was obtained by summation of the maximum number of pairs (singing male = pair) of each passerine (Enemar 1959), and woodpecker species. When there was a large discrepancy between counts, averaging or counting nests determined the count. Not included in the summation were Pine Siskins (*Spinus pinus*), Brown-headed Cowbirds (*Molothrus ater*) and hummingbirds because of their unusual behavior, Goldfinches (*Spinus tristis*) and Cedar Waxwings (*Bombycilla cedrorum*) because of late breeding, and species with large territories. High counts made during migration were excluded.

Surveys were conducted between 5 May and 12 July, and each stand, with the exception of No. 19, had one survey during June near the peak of the breeding season. Calm, fair days were considered necessary for the counts to be comparable.

The use of a bird census made during the breeding season must be approached with caution. Enemar (1959) has pointed out that census methods are directed towards four types of populations. The breeding population can be determined only by finding all nests, while the stationary population is determined by mapping territories. Strip surveys determine the total population, but summation of the results of several surveys introduces a distortion in the proportions of the species represented.

Since this study demanded that a large area be surveyed, I could make only two counts in any one stand. Enemar (1959) found in his analysis of a long narrow study area (13 hectares) with a dense population, that on the average 60 percent of the stationary population is registered at each survey, and after two surveys 84 percent of the population has been registered once. Bond (1957) checked the sample count method against the more intensive spot map method of Kendeigh (1944) on three plots, and found his own sample counts 22 to 30 percent lower than spot map counts. Emlen (1971) reviews the problems in various census methods and presents a new method for obtaining absolute counts efficiently.

There are a number of sources of error in the method used. Differences in conspicuousness between species should remain constant from area to area, except as it is affected by density of vegetation. However, changes in the behavior of species as the season progresses, as with juncos, probably had an effect on results. The chance of recounting a bird was reduced through caution and by the 75-foot separation between strips. Both aural and visual detection of species assured less error in separation of singing males from females. The number of unmated nonbreeding males in a population can be large (Lack 1937), but should be comparable in the stands. Transient birds could not often be detected but their numbers should also be comparable from stand to stand. In a few cases when a species was recorded early in the season, but not at the peak, and not detected upon later observation, it was not included in the summation. Speed of movement along the transect was relatively constant, as was weather and time of day of surveys. Some stands were surveyed in early and middle June, while others were surveyed in middle June and late June or early July. The potential error here due to changes in the populations is not systematic. A single observer carried out all surveys, and his familiarity with each stand and the species present prior to survey was enhanced during visits to choose and mark the stand and analyze the vegetation. This experience demonstrated to the author that few species were missed in the counts. Familiarity with each stand and the well-marked transects assured greater effectiveness of the surveys.

In stands 20–27, in which the arrangement of the strip varied, errors made will probably differ somewhat from the other surveys. Also, possible yearly fluctuations in bird populations introduces season to season variation.

No census method is without sources of error and disadvantages, or without worth as long as it is completely described and consistently applied (Enemar, 1959). With these reservations in mind, the data are used for comparison of abundance of species and total populations between stands.

The question of the absolute size of populations cannot be safely considered without knowing the reliability of the method.

SELECTION WITHIN THE HABITAT

During late April and May the birds arrive in the stands and begin pair formation, exhibit territoriality, and search for suitable nest sites. Arrival dates differ among species by as much as a month, but stands in the western mountains are well settled before leafing-out of the trees occurs, and before the shrubs and herbs have shown much growth. In Canada leafing-out often occurs during or just prior to the arrival of many species. Whether an individual exhibits philopatry (Welty 1962: 225; Mayr 1963: 670) or, alternatively, arrives at a stand for the first time, the habitat in spring often differs greatly in appearance from that in which it fledged or from which it migrated the previous summer. In the case of species that glean insects from leaves, a most important feature of their environment is completely absent.

Surrounding forests (coniferous) are physiognomically different and branches are covered with needles. It is possible, then, that individuals react, either by genetically determined processes or by those modified by experience, to prominent differences in physiognomy (leafless deciduous forest) when locating an appropriate breeding habitat. It does not seem likely that sorting of species into different habitats at this time occurs through interspecific interactions. Parnell (1969) has shown that many migratory warblers prefer habitats similar to the breeding habitat. It is also possible that species make a choice on the basis of more specific structural (or other) features of a habitat that are important to protection, territorial behavior, nest construction, or feeding. This process could occur in conjunction with habitat selection on the basis of physiognomy. Finally, it is evident that under certain conditions environmental factors other than habitat structure and physiognomy influence habitat selection (Root, 1967).

Throughout the following discussion stand 34, located near Rochester, Alberta (≃ 54°N), in the mixed boreal forest, is singled out because it so often did not fit patterns common to most other stands. The unique geographical position of this stand appears to have given rise to the differences. It may be argued that differences in this single stand were due to chance. However, every guild (Root 1967) showed striking changes in density or composition and the other forests in the area that the author walked through gave a similar impression. Then too, the accounts of Soper (1949) in this region and similar areas to the north and west in Alberta, the descriptions by Munro and Cowan (1947) for the Peace River parklands, and those of Rand (1944) along the Alaskan Highway confirm, as well as descriptive studies are able, the gradual reduction in the number of bird species in aspen forests as one moves northwest from the parklands of Alberta. Some species appear to be replaced geographically by a similar form that itself may eventually be lost. Some of these changes are treated in the last section of this monograph. The forests are structurally very similar to those of the parkland and southern poplar forests. Drury (1953) has described the bird species and their abundance in aspen groves in the southwestern Yukon Territory, and although he remarks on the comparative richness in species of this habitat, the total number of species breeding, and their abundances, are low in comparison to parkland. Composition is very different and certain guilds are almost absent. Williamson (1957) describes a similar reduction in number of bird species in Alaskan spruce forests along a generally east-west gradient.

The stand (34) may characterize general differences between the southern mixed boreal forest and the parkland, although a single stand cannot represent that region. Structurally the stand was similar to other mature aspen forests with moderate shrub cover. The rich litter, however, seemed less subject to drying out. *Populus balsamifera* was more numerous than in most but not all parkland stands. Frosts may continue into mid-June and the growing season (those weeks above forty-two degrees Fahrenheit mean) is shorter in this region (Longley 1967). Rainfall may be somewhat less than in the parkland, but moisture stress is considerably less. Variability in precipitation is less (Currie 1953). The presence of a few paper birch (*Betula papyrifera*) and spruce (*Picea glauca*) in the stand in part reflected these differences.

A total of 14 species and 79 individuals were recorded in stand 34 (10 and 70 in summation) in contrast to the 20 to 28 species and 104 to 147 individuals recorded in stands of similar tree density and dbh in the parkland (Table 1). In the canopy the Baltimore Oriole (*Icterus galbula*) was uncommon and the American Goldfinch (*Spinus tristis*) and the Western Wood Pewee (*Contopus sordidulus*) were not recorded. The latter two species are uncommon or rare in the region (Soper 1949). Orioles are absent further west (Munro and Cowan 1947). The only abundant species recorded was the Least Flycatcher (*Empidonax minimus*).

Among shrub nesting species, the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) was conspicuously absent. The Yellow Warbler (*Dendroica petechia*) nested in a nearby area. House Wrens (*Troglodytes aedon*) were also conspicuous by their absence, and no cavity dependent species were present in spite of the abundance of woodpecker cavities. The Pileated Woodpecker (*Dryocopus pileatus*) is more common in this part of the mixed boreal forest than in the parkland, and its workings were seen throughout the stand.

Ground nesting birds were abundant, a difference partly substantiated by Soper (1949) and Weatherill and Keith (1970). Ovenbirds (*Seiurus aurocapillus*) were more than two times as numerous as in the parkland, and the

TABLE 1

BREEDING BIRDS OF ASPEN FORESTS
SUMMARY DATA FOR ALL STANDS SAMPLED, 1966–1969

	Relative abundance in each stand									
	Arizona					N. M.		Colorado		
Birds by nesting guild†	1	2	3	4	5	6	7	8	9	10
Canopy										
Western Wood Pewee	8	8	14	4			8	8	4	8
American Robin	8	8	4	6		2	6	10	10	8
Warbling Vireo	16	10	14	10	12	12	12	14	14	14
Audubon's Warbler	12	6	10	2		4	8	8	8	8
Western Tanager				2						
Evening Grosbeak	2		4	6						
Cassin's Finch										2
Shrubs										
Empidonax flycatcher		2	4	4			2	6	4	4
Black-headed Grosbeak			2	2			2	2		
Chipping Sparrow	4	2		2			2			
Song Sparrow										2
Holes										
Red-shafted Flicker			4	2				2		2
Yellow-bellied Sapsucker		2		2						
Hairy Woodpecker	2									
Downy Woodpecker	2		2	2			2			
Violet-green Swallow	6		12	4						6
Black-capped Chickadee										2
White-breasted Nuthatch	2									
Pigmy Nuthatch			2							
House Wren	8		14	6			6		4	10
Western Bluebird	4	2	4							
Mountain Bluebird	4	2	4	2			2	6	4	2
Ground										
Hermit Thrush	2	2	2	2	4	4	4	2	2	2
Townsend's Solitaire							2			
Gray-headed Junco	4	4	4	2	4	6	6	4	6	6
Summation Totals										
No. species	15	11	17	16	3	5	13	10	9	14
No. individuals	84	48	102	58	20	28	62	62	56	76
Others										
American Kestrel			P							
Great Horned Owl			2							
Long-eared Owl							2			
Broad-tailed Hummingbird	6	2	2	2	2	1	4	2	1	1
Brown-headed Cowbird	4	2	1	2						
Pine Siskin	2		2			3		2	2	4

TABLE 1 (continued)

	Relative abundance in each stand								
	Colo.		Utah						Cal.
Birds by nesting guild†	11	12	13	14	15	16	17	18	19
Canopy									
Western Wood Pewee	4	2	8	6	10	8	4	4	8
American Robin	6	8	6	8	8	12	8	8	8
Warbling Vireo	14	8	14	12	14	10	6	12	14
Audubon's Warbler	6	10	8	8	6	6	4	6	
Cassin's Finch	4		2	2	4	6	6	4	6
Shrubs									
Empidonax flycatcher	4			2	2	4	2	6	12
Yellow Warbler	2								
MacGillivray's Warbler		8							
Black-headed Grosbeak			2		2		2		4
Lazuli Bunting								2	
Green-tailed Towhee	2								6
Chipping Sparrow			6	4	6		4		
Song Sparrow		2				8		2	
Holes									
Red-shafted Flicker		2	4	2	6	4	4	2	4
Yellow-bellied Sapsucker	2					2		2	
Red-bellied Sapsucker									2
Hairy Woodpecker			2		2		2		
Downy Woodpecker					2	2			
Violet-green Swallow				4	8	8	4		
Tree Swallow			3		10	46		10	
Purple Martin						8			
Black-capped Chickadee	2	2						2	4
House Wren	4	6	2		8	8	2	6	14
Mountain Bluebird			6	2	6	8	4	2	8
Starling						2			
Ground									
Hermit Thrush	2	8	4	4				2	2
Townsend's Solitaire									2
Oregon Junco									10
Gray-headed Junco	10	16	12	4	10	10	6	8	
White-crowned Sparrow						20	30	30	2
Lincoln's Sparrow						2			
Summation Totals									
No. species	13	11	14	12	16	19	15	17	16
No. individuals	62	72	78	58	104	174	88	108	106
Others									
Great Horned Owl				2	2				
Broad-tailed Hummingbird	6	6	5	7	5	5	14	3	
Brown-headed Cowbird									4
Pine Siskin	10	6	14	6	8	12	4	2	2

TABLE 1 (continued)

	Relative abundance in each stand							
	Wyoming							
Birds by nesting guild†	20	21	22	23	24	25	26	27
Canopy								
Western Wood Pewee		2	8	4	8	4	4	4
American Robin		2	2	2		6		12
Warbling Vireo	12	12	12	16	8	6	6	14
Audubon's Warbler		2	2	2	4	2		2
Western Tanager						2		
Cassin's Finch						4		2
American Goldfinch								2
Shrubs								
Empidonax flycatcher	8	8	12	10	14	8	12	12
Yellow Warbler	4	6	4	4	6		6	20
MacGillivray's Warbler			2		2			
Black-headed Grosbeak	2						2	2
Chipping Sparrow				2		4		2
Holes								
Red-shafted Flicker			4	4	2	4	4	4
Yellow-bellied Sapsucker				2				
Hairy Woodpecker				2		2		
Downy Woodpecker					2		2	
Tree Swallow			10	8	6	6	6	8
Black-capped Chickadee	2	2	4	4	4		2	2
House Wren		4	4	12	4	6	8	8
Mountain Bluebird			4	6	4	4	2	2
Ground								
Pink-sided Junco	12	8	6	16	8	8	4	6
White-crowned Sparrow			4	2	8			
Summation Totals								
No. species	6	9	14	16	14	14	12	16
No. individuals	40	46	78	96	80	66	58	102
Others								
Red-tailed Hawk		P		P				
American Kestrel					P		P	
Ruffed Grouse	2			1		1		1
Great Horned Owl	2	2						
Common Raven					P		P	
Brown-headed Cowbird		2	2					
Pine Siskin	2		1			12	2	9

TABLE 1 (continued)

	Relative abundance in each stand						
	Foothills			Parkland			Boreal
Birds by nesting guild†	28	29	30	31	32	33	34
Canopy							
Eastern Kingbird			2		2		
Least Flycatcher	22	6	24	24	36	34	28
Western Wood Pewee		6	4	2	4		
American Robin	4	2	8	4	12	6	4
Red-eyed Vireo	6	4	2	4	4	4	8
Warbling Vireo	4	2	4	2	2	4	
Baltimore Oriole		4	4	6	14	12	2
Western Tanager	2						
Shrubs							
Black-billed Cuckoo	2						
Empidonax flycatcher	2	2					
Gray Catbird	2		2				
Yellow Warbler	12	4			16	8	
Rose-breasted Grosbeak				4	2	4	
Black-headed Grosbeak	6						
Chipping Sparrow		8	2				
Clay-colored Sparrow	2			4			
Holes							
Yellow-shafted Flicker				2			
Red-shafted Flicker	2	2					
Pileated Woodpecker	2			P			P
Yellow-bellied Sapsucker	2	2		2	4		2
Hairy Woodpecker							2
Downy Woodpecker	2	2	2		2		
Black-capped Chickadee		4	2	4	4	2	2
Red-breasted Nuthatch	2	2	2	2			P
House Wren	18	14	10	10	20	10	
Mountain Bluebird	P		P		P		
Ground							
Hermit Thrush			2	2		2	4
Veery	12	8				6	
Ovenbird			6				14
Connecticut Warbler				P			P
White-crowned Sparrow	6	2					
White-throated Sparrow				4	4	4	4
Summation totals							
No. species	19	17	15	15	14	12	10
No. individuals	110	74	76	76	126	96	70

TABLE 1 (continued)

	Relative abundance in each stand						
	Foothills			Parkland			Boreal
Birds by nesting guild†	28	29	30	31	32	33	34
Others							
Red-tailed Hawk	P		P				
Broad-winged Hawk							P
Ruffed Grouse	2	2	1	1	3	1	1
Great Horned Owl		2					
Long-eared Owl					2		
Cedar Waxwing	4	7	6	1	3	6	2
Brown-headed Cowbird	10	5	5	2	5	9	5
Pine Siskin	9	11	5	15			
American Goldfinch	3	3	2	2	2	10	

	Relative abundance in each stand						
	Parkland						
Birds by nesting guild†	35	36	37	38*	39	40	41
Canopy							
Lesser Yellowlegs	4						
Eastern Kingbird					2		
Least Flycatcher	28	32	14	6	30	34	36
Western Wood Pewee	10				2		
American Robin	10				2		
Red-eyed Vireo		6	6		8	10	4
Warbling Vireo	6	4		12	8	6	4
Baltimore Oriole	14	10			10	8	2
Common Grackle	4						
Purple Finch					4		
Shrubs							
Black-billed Cuckoo							2
Gray Catbird						2	2
Yellow Warbler	14	4		4	12	20	4
American Redstart			2			8	4
Rose-breasted Grosbeak	6	2			6		6
Rufous-sided Towhee					2		2
Chipping Sparrow			2				
Clay-colored Sparrow		2	2	4		2	
Song Sparrow	6	2				2	

TABLE 1 (continued)

	Relative abundance in each stand						
	Parkland						
Birds by nesting guild†	35	36	37	38*	39	40	41
Holes							
Yellow-shafted Flicker	2						
Pileated Woodpecker	P				2	P	
Yellow-bellied Sapsucker	6	2			4		
Hairy Woodpecker		2			2		
Downy Woodpecker	2				2		2
Great Crested Flycatcher			2		4	2	
Tree Swallow	4				2		
Black-capped Chickadee		2			4	2	2
Red-breasted Nuthatch		P				P	
House Wren	12	2	2	2	10	8	4
Ground							
Hermit Thrush			2				
Veery			4		2	10	6
Ovenbird		6	6				2
Connecticut Warbler					P		
Mourning Warbler					2	2	
Summation Totals							
No. species	16	14	10	5	22	14	16
No. individuals	134	80	42	28	122	118	84
Others							
Red-tailed Hawk	2						
Broad-winged Hawk	P	P			P	2	
Ruffed Grouse	1	1	1	2	6	2	4
Great Horned Owl					P		
Cedar Waxwing			1	2	5	1	3
Brown-headed Cowbird	19	10	3	4	6	2	11
American Goldfinch			1	10	2	5	3

Abbreviations: N. M. = New Mexico, Colo. = Colorado, Cal. = California, Foothills = Foothills of parkland in Alberta, Boreal = southern boreal region of Alberta, P = present in similar adjacent habitat. † Guilds are composed of species showing similarities in environmental exploitation (Root, 1967); *others*, the last grouping of birds for each locality is not a guild. It records birds that could not be included in the summation, as described in the text under methods. * Stand 38 was large enough for only one-half of a transect; recorded abundances were doubled except for the House Wren whose high relative abundance was disproportionately influenced by favorable habitat on edges.

Hermit Thrush (*Catharus guttatus*) and White-throated Sparrow (*Zonotrichia albicollis*) were common. Connecticut Warblers (*Oporornis agilis*) also nested in the area.

The composition and density of stand 34, with the exception of ground nesters, suggested a depauperate parkland avifauna. This stand had the lowest diversity index of any mature forest from Arizona to Manitoba (Fig. 1 and 2). It may prove to be of some relevance that there is a similar abrupt change in bird diversity at 20–25° latitude in central America, a phenomena that may also be associated with certain climatic thresholds (Klopfer and MacArthur 1961; Tramer 1968).

COMPARISONS BETWEEN REGIONS

The higher total number of breeding species recorded in the parkland stands than in the western mountains appears to be a result of several historical, geographical and ecological factors some of which are discussed later. The greater number of species and individuals found in a given stand in Canada in contrast to the western mountains (Fig. 3 and 4, Table 1) receives more attention here.

The first point to examine is whether stands in the two regions are actually structurally similar, because a structurally more diverse stand might be expected to attract more birds. Stands in both regions are dominated by essentially pure aggregations of *Populus tremuloides*, although in both regions several species of conifer may occur in low numbers. In Canada another poplar, *P. trichocarpa*, occurred in stand 28 in southwestern Alberta and *P. balsamifera* occurred in eight other stands, and in the two most eastern stands (40 and 41) an oak, *Quercus macrocarpa*, and an ash *Fraxinus pennsylvanica* were found in low numbers. This would suggest that the Canadian forests are more diverse structurally because of the presence of these additional types of trees. However, most stands include few or none of these additional trees, and with the exception of *P. balsamifera* none were represented by more than a few individuals. Of the nine stands having an additional poplar, in only four (Nos. 34, 35, 36, 39) did the total number of trees exceed five percent, most individuals having been in clumps in one or two places. A greater range of forest densities were present in the mountains. There, tree dbh and height also often reached greater proportions than in Canada, and stands in Canada showed much greater homogeneity for tree dbh. The tallest forests averaged 59 feet in Canada and 70 feet in the mountains, while the maximum thickness of the canopy in both regions was 28 feet.

There was a great deal of overlap in the two areas with regards to amount of shrub cover and the species of shrubs present. Cover in the western mountains ranged from none in the south to 19% in Wyoming while that in Canada ranged from 8 to 46%. Dominant shrub species in the two areas were variable but typically different. Stands in Canada with very dense shrub cover were not studied because of the great difficulty in moving through them.

The ground cover in the two regions is always a mixture of grasses and forbs with varying amounts of litter covered bare earth. Stands in the western mountains could have as much as 68% grass or 94% forbs, compared to a maximum of 30% grass or 75% forbs in Canada. Ground covered only by a thick layer of litter comprised a greater percent of the cover in Canada.

In summary, the differences between the two regions are mainly floristic

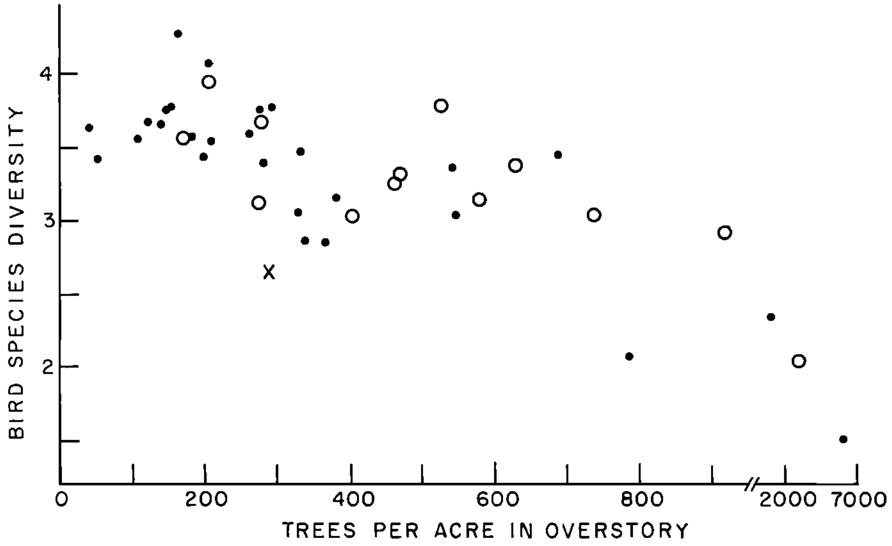


Figure 1. Bird species diversity (H′ Shannon-Weiner) in relation to tree density. Dots = stands 1–27; open circles = stands 28–41; X = stand 34. This system pertains to all figures with exceptions noted.

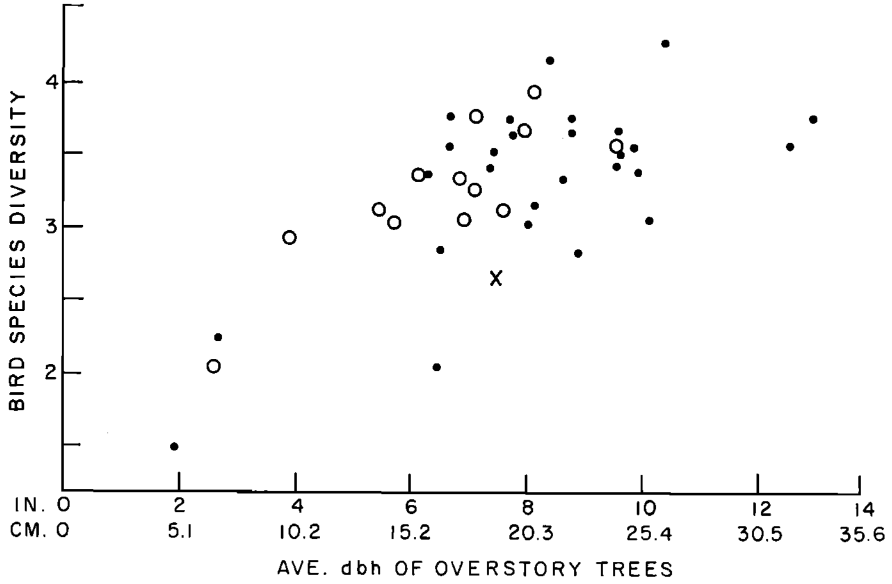


Figure 2. Bird species diversity (H′) in relation to average tree diameter at breast height.

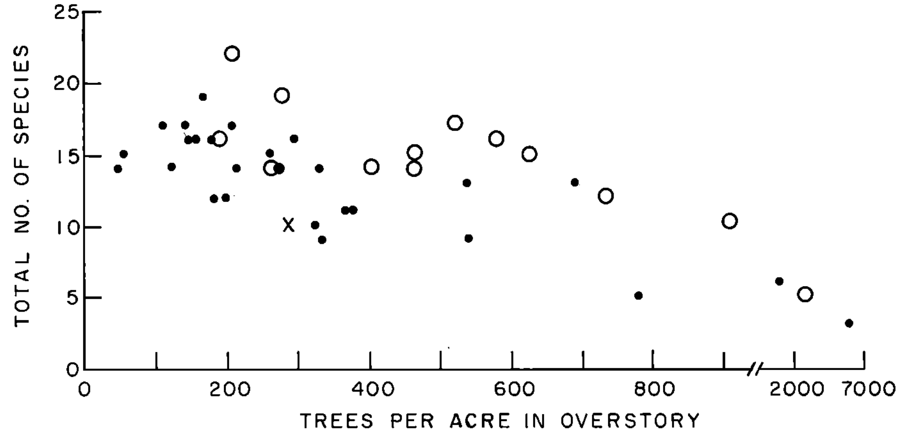
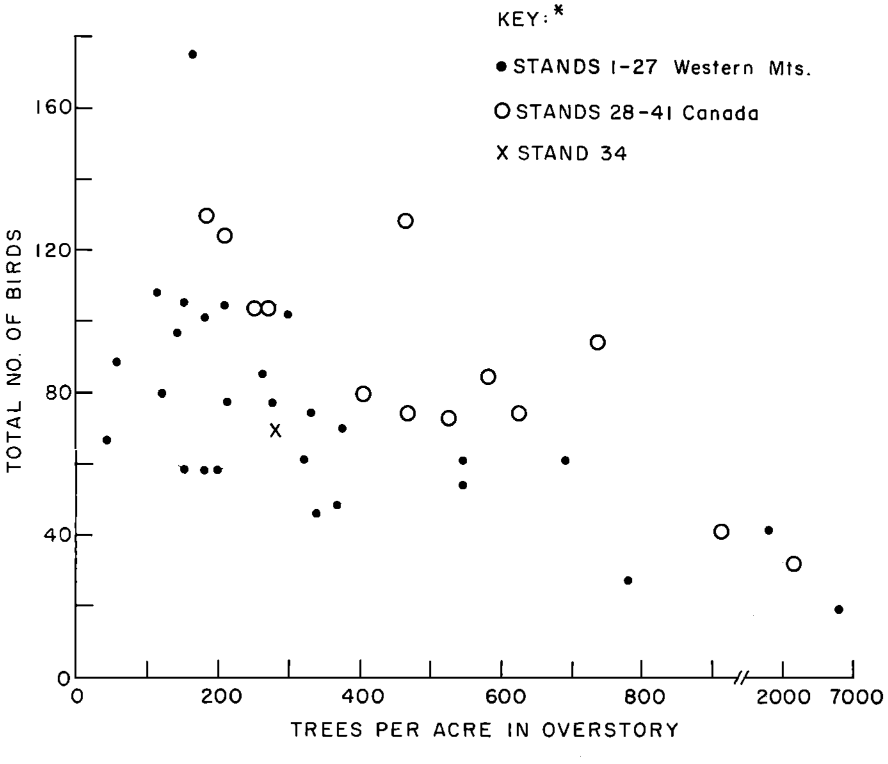


FIGURE 3. The total number of bird species in the summations in relation to tree density.

in nature, and do not give rise to forests that differ greatly in structure. In the two regions forests of similar tree density and variable amounts of shrub and herbaceous cover are often almost indistinguishable on the basis of structure.

In contrast to the structural similarities of stands in the two regions, there are several climatic features that distinguish all the stands in the western mountains (1–27) and foothills (28–30) from stands 31–41. In any of the stands 1–30, frosts occur in the breeding season, and nights are always cold, in contrast to the warmer nights in the parkland. Stands 1–27 leafed out later by up to two weeks than stands 28–41, probably reflecting a later and shorter growing season but complicated by clonal differences (Cottam 1954).

The entire parkland region receives most of its precipitation just prior to and in the growing season, June or July being the wettest months (Currie 1953; Kendrew and Currie 1955). The mountain areas are much drier during this time, the greatest amount of precipitation coming as snow in winter. This varies greatly with topography and from south to north with roughly 2–4 inches (5.1–10.2 cm) falling in April and May and 3–5 inches (7.6–12.7 cm) in June and July (USDA 1941). In the parkland precipitation is greatest during the growing season (April–July). The mean annual rainfall for this period ranges from 7–10 inches (17.8–25.4 cm), Manitoba receiving over 10 inches (Currie 1953). With the periodic drought in the parkland, summer precipitation is much lower, but the western mountains have a higher frequency of summer drought (USDA 1941). Edaphic and exposure factors greatly complicate moisture relationships, but these were highly variable in both regions.



*Key applies to all graphs unless otherwise indicated.

FIGURE 4. The total number of birds in the summations in relation to tree density.

It follows from the above discussion that warmer nights and moister summers are the only important differences that distinguish parkland stands from those in the western mountains. It is not clear, however, that this difference is the sole correlate of the higher populations of birds in Canada (Figs. 3, 4, 5, 6 and Table 1). Geographical and historical factors are considered in following sections.

The changes in bird populations that occur from the foothills to the lower elevations of the parkland and between the boreal region (34) and the parkland are significant because the habitat is essentially continuous between areas at different ends of a climatic continum. In addition, numerous changes in the understory plant species occur between these areas (Moss 1955; Bird 1961). The greatest avifaunal transition, that between stands 1–27 and 28–41, coincides with a major geographic discontinuity in the aspen forests (frontispiece) and with climatic differences between the two areas. They are discussed in the following sections.

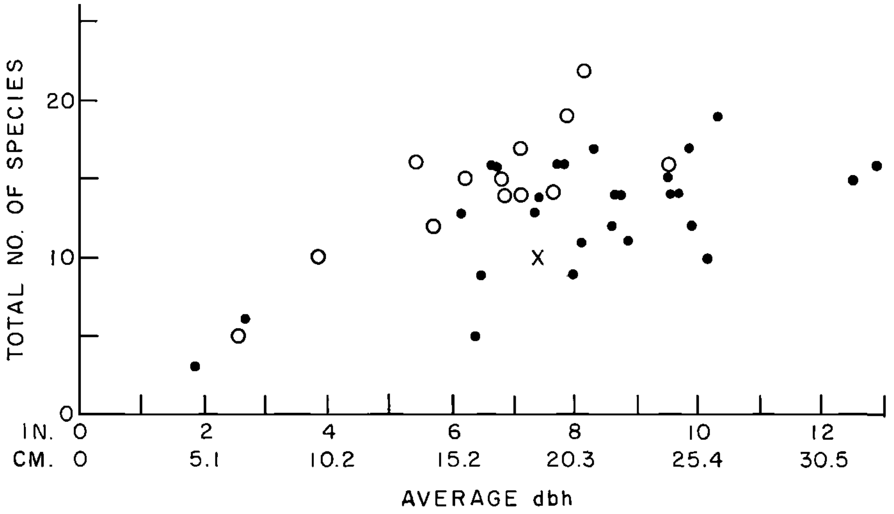


FIGURE 5. The total number of bird species in the summations in relation to average tree diameter at breast height (dbh).

A total of 45 breeding species were recorded in stands 1–27 in the western mountains, the maximum number found in any one stand was 21 (16) and the minimum 4 (5). This contrasts with stands 28–41 in Canada where 56 breeding species were recorded, the maximum number found in any one stand being 28 (39) and the minimum nine (38). Two species widely distributed in parkland aspen were not recorded in any stand but occurred in numerous adjacent forests. Frequency and abundance values for species are listed in Tables 1 and 8.

Data from the population summations were used to examine relationships of species composition and abundance to forest structure. Because of the necessity of including only species amenable to summation methods in these quantitative comparisons, information was lost. In Canada 10 excluded species that bred in the stands, including 4 abundant species, boost total densities by a considerably larger amount (20–28 individuals in each of 8 stands) than the 8 similarly excluded species in the western mountains (4–8 individuals in most stands), which includes 3 that were common (Table 1). The species involved in both regions are exclusively inhabitants of the canopy, except the Ruffed Grouse (*Bonasa umbellus*) and Brown-headed Cowbird (*Molothrus ater*).

Several correlations between single species and vegetation are described. A stand was not plotted on the graph in those cases where the species was both totally absent in the stand and also absent or rare in the surrounding area. Only those relationships clearly showing trends are examined.

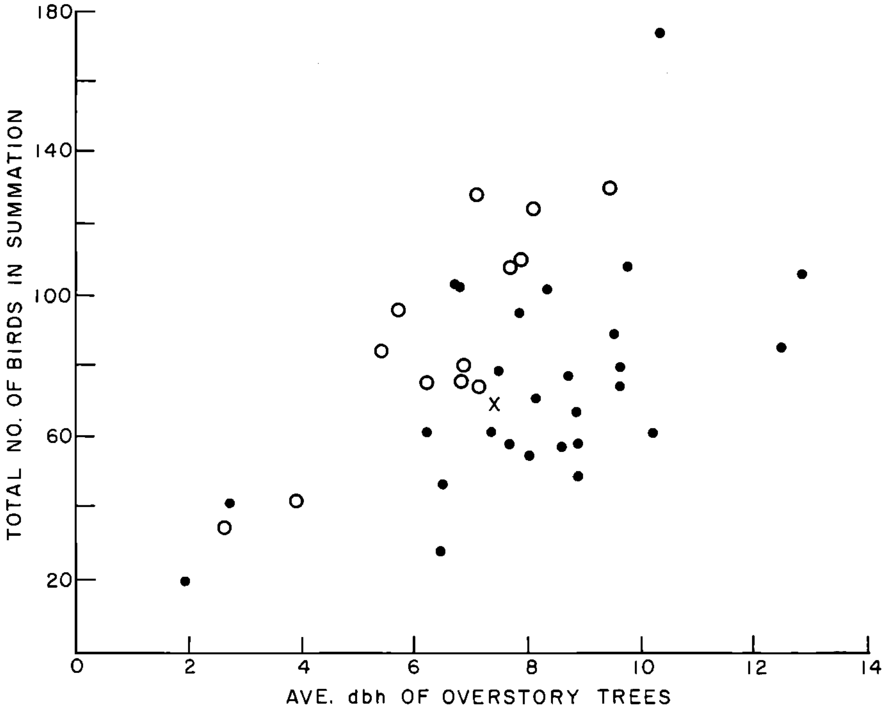


FIGURE 6. The total number of birds in the summations in relation to average tree diameter at breast height.

It has been useful to relate guilds, composed of species showing similarities in environmental exploitation (Root 1967) to certain structural features of the forests. Haapanen (1965) has used similar ecological groupings. Comparisons are usually between stands in the western mountains (1–27) and stands in Canada (28–41), although stands 20–27 in Wyoming are occasionally omitted or considered separately.

On the basis of choice of nest site, five distinct guilds may be formed. I found that several species located nests on small twigs and small branches in the canopy (guild 1), while others built on large tree branches and forks in and below the canopy (guild 2). Guild 3 includes species nesting in shrubs, guild 4 includes hole nesting birds and guild 5 those species nesting on the ground. Assignments were made on the basis of my findings in the field and references to Bent (1919–1968) and to Salt and Wilk (1966). *Empidonax* flycatchers in the mountains generally nested in shrubs, occasionally nested in the canopy of small trees and in stand 19 nested exclusively in trees (average height to bottom of canopy 11 ft). Least Flycatchers nested in trees. The Red-eyed Vireo (*Vireo olivaceus*) nested in trees and shrubs, as did the Chipping Sparrow (*Spizella passerina*).

When grouped by feeding site, guilds were not always mutually exclusive, but seven have been recognized. Species feeding by gleaning in the canopy comprise guild 1a, and those gleaning in both the canopy and shrubs, guild 2a; shrubs only, guild 3a, on and under bark, 4a, hawking and flycatching below the canopy, 5a, continuously on the wing, 6a, and on the ground, 7a. Not all of these activities occurred within the confines of a stand. I assigned species to these categories on the basis of field observations. Bluebirds were assigned to guild 5a.

When species are combined into guilds, a certain amount of information is lost concerning their individual requirements. On the other hand, habitat use for each species was not quantified, and correlations of an individual species abundance with average values for vegetation parameters were not very successful. Sampling vegetation within known bird territories is exceedingly time consuming and does not yield results that distinguish between minimum and maximum stimuli for territorial establishment (Sturman 1968a).

Correlation of a structural feature with the composition or density of the bird populations in that environment could be the result of the structural feature being of immediate or proximate importance in the breeding season or at the time of selection of a breeding habitat. On the other hand it could be of no importance if that feature is only correlated to the factor or factors of significance. Strictly fortuitous correlations in a complex environment are unlikely. Unfortunately, in this study one can only speculate upon the significance of the correlations found.

The number of bird species in a stand decreased with increased overstory tree density (Fig. 3). The number of individuals correlated in a similar way with tree density, although there was a greater spread of points (Fig. 4). In both cases there was an indication of a slight drop in number in stands with fewer than 100 trees per acre. Throughout the range of tree densities, numbers of species and individuals from stands in Canada, excepting stand 34, averaged higher than in the western mountains. Stand 34 in Canada showed conspicuously low values and was the only stand located well within the boreal forest region of Canada. Other deviations of this stand (34) are noted elsewhere.

Shannon-Weiner species diversity values, H′, are discussed more fully in a later section. When they are plotted against either tree density or dbh, stands in the two regions show great similarity (Figs. 1, 2). If diversity is calculated on the basis of nesting guilds, values are nearly constant through a wide tree density range, and values for stands in Canada average slightly lower than those in the western mountains (Fig. 7).

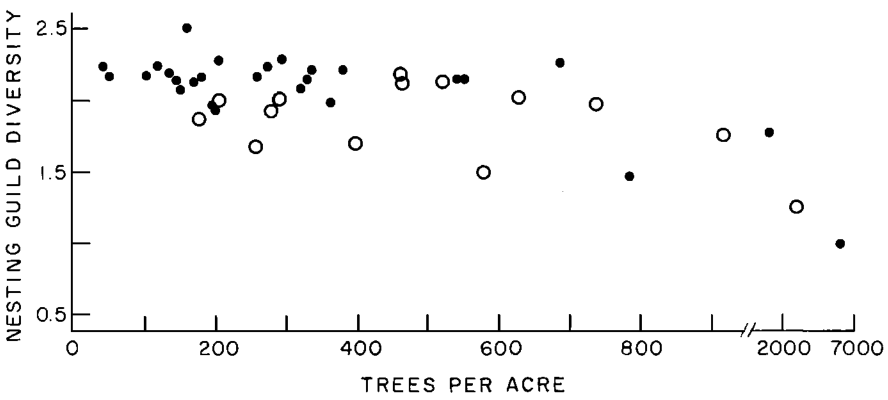


FIGURE 7. Nesting guild diversity in relation to tree density. See text for explanation of guilds.

Udvardy (1958) suggests that tree density is an important determinant of of bird density. The correlations of numbers of species and numbers of individuals and of bird diversity with tree density may indicate that this has validity in some communities. In the east, comparable values of H′ are found in deciduous forests of much lower tree density and greater tree size (Tramer 1968). It is probable that tree density is correlated with a number of structural features of more immediate importance to species. In the case of several species and guilds it will be seen that tree density or dbh is of no significance, but that this is masked by the larger numbers of correlations with tree density and dbh.

Bird species diversity has been shown by many authors to increase with the number of layers of vegetation, the completeness of these layers, and the patchiness of the layers. Mature aspen forests in the southern Rocky Mountains frequently lack a shrub layer and are therefore structurally less diverse than shrubby stands. The bird species diversity of numerous such shrubless forests (1, 3, 4, 13–15, 25) was as high (H′ average = 3.684) as in very shrubby forests in the parkland and other temperate deciduous forests and was much higher than in two-layered habitats (Tramer 1968). In following sections it will be shown that a number of factors other than foliage diversity also influence bird species diversity of aspen forests.

As tree diameter at breast height (dbh) increases, numbers of species and total bird density increase (Figs. 5, 6). Stands in Canada again showed higher bird densities at most tree diameter sizes than stands in the western mountains. In the latter two figures the spread of points is greater in stands 1–27. These stands, unlike those in Canada, were characterized by great heterogeneity in tree dbh, but plotting only the most homogeneous montane stands does not decrease the spread.

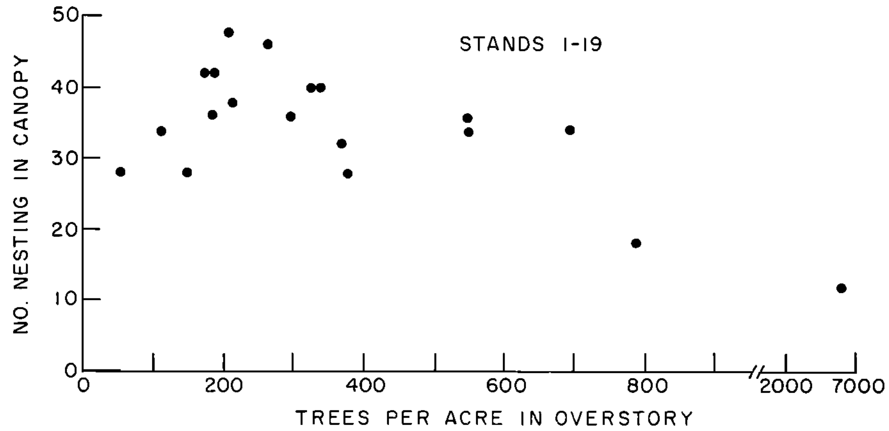


FIGURE 8. The number of birds nesting in the canopy (guilds 1 and 2) in relation to tree density in stands 1–19.

The better correlation between bird densities and tree dbh that is seen for stands 28–41 (Figs. 5, 6) than for stands 1–27, may simply be a result of chance and a smaller sample size, but may be due to the structure of the forests themselves. Stands 28–41 were extremely homogeneous for tree dbh, as shown by plots of dbh against density, which closely approximate normal curves. Most stands in the western mountains were bi- or multimodal, reflecting multi-aged forests. As discussed below, certain groups of birds, notably cavity nesters, were most responsible for the difference in correlation.

THE CANOPY

The number of birds nesting in the canopy (guilds 1 and 2) in stands 1–19 decreased with increased tree density but were low at lowest tree densities (Fig. 8). The number of birds nesting on large limbs (guild 2) showed a very similar pattern (Fig. 9). The number of species in these guilds was rather constant throughout a great range in tree density with a decline above 700 trees/acre (Fig. 10). In Canada the number of birds nesting in the canopy increased with increased average thickness of the canopy (Fig. 11), and showed no correlation with tree density. Yet the number of birds in these guilds also correlated with average height to the top of the canopy (Fig. 12). Canopy thickness is roughly correlated with height in Canada (Fig. 13). Correlations of these guilds with tree density, dbh or percent cover of the canopy were not found in Canada.

The constancy in number of individuals and species constructing nests on tree twigs, branches and forks (guilds 1 and 2; Figs. 8, 10) in stands varying from 54 to 800 trees per acre was probably a direct reflection of

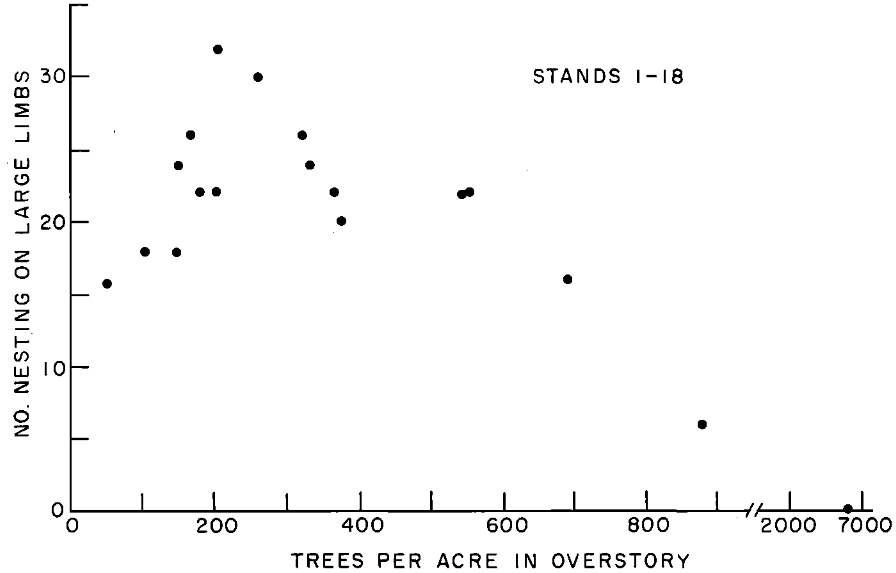


FIGURE 9. The number of birds nesting on large limbs (guild 2) in relation to tree density in stands 1–18.

the availability of nest sites. Aspen trees change little in structure but simply increase in size as they grow. Forests of more than 800 trees per acre are composed of small trees lacking heavy branches and forks. Limb nesting birds (guild 2, Fig. 9) alone suggest that available forks and large branches are most abundant when tree density is between 150 and 300 trees per acre, where large trees are most abundant. Eighty-six % of the 14 nests of pewees found were located on heavy, short dark horizontal branch stubs that occurred beneath the crown only on large trees. This was reflected in the re-

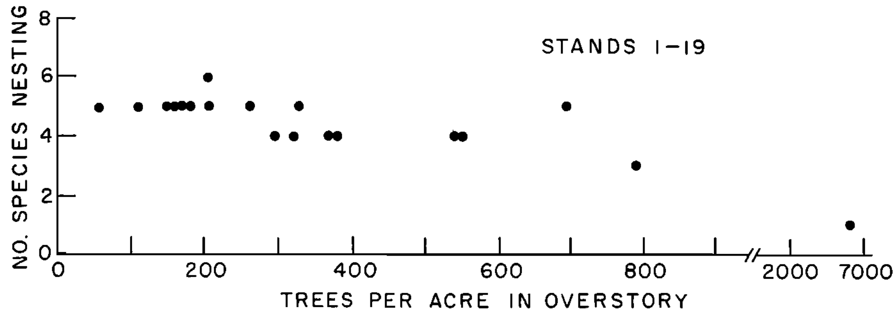


FIGURE 10. The number of species nesting in the canopy (guilds 1 and 2) in relation to tree density.

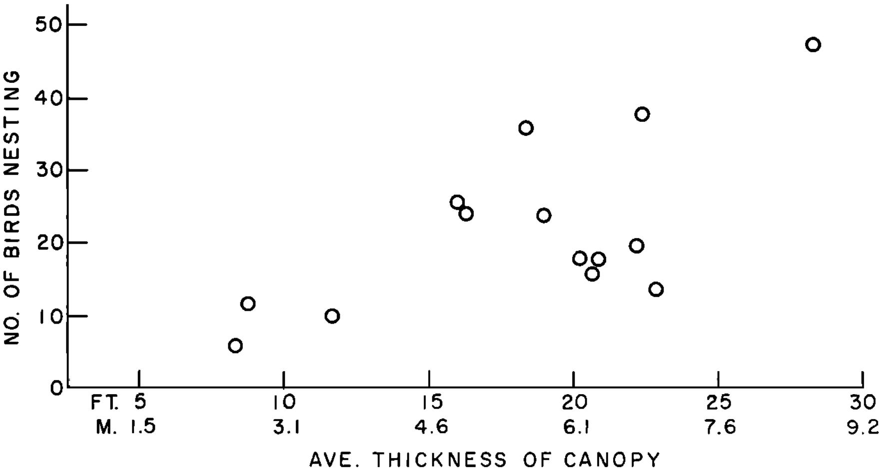


FIGURE 11. The number of birds nesting in the canopy (guilds 1 and 2) in relation to average thickness of the canopy in stands 28–41.

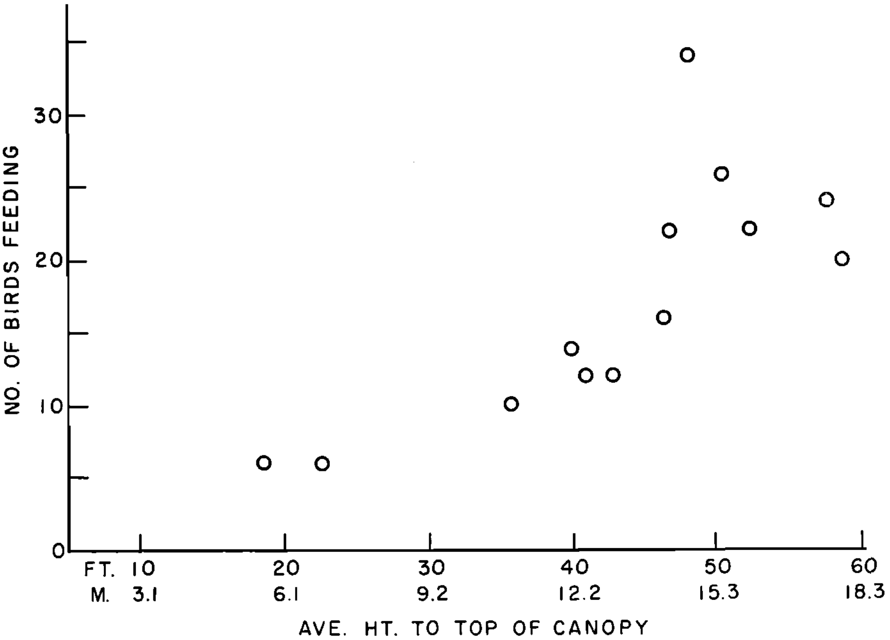


FIGURE 12. The number of birds feeding in the canopy by gleaning (guild 1a) in relation to average height to the top of the canopy.

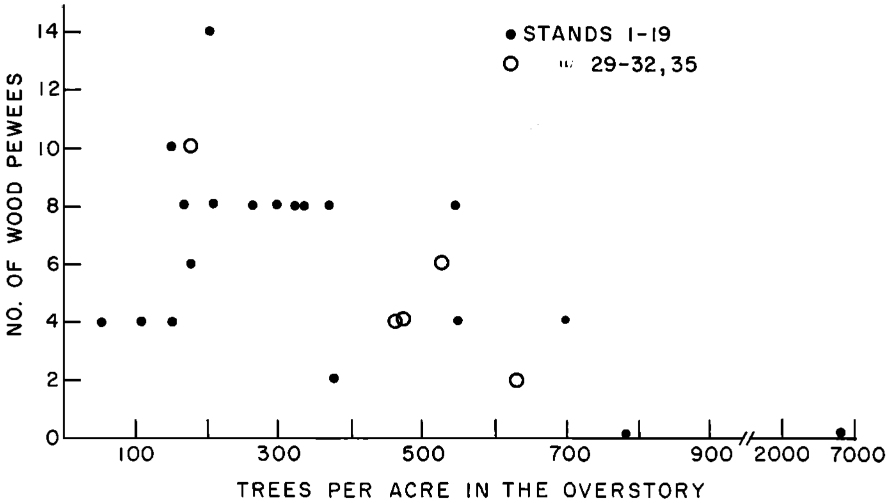


FIGURE 13. The number of Western Wood Pewees in relation to tree density.

lation of pewee density to tree density (Fig. 13) and tree dbh (Fig. 14). Similarly Robins (*Turdus migratorius*) most often built nests in large tree forks or on large limbs or limb scars (80% of 28 nests). Their density increased with tree dbh in stands 1–18 (Fig. 15).

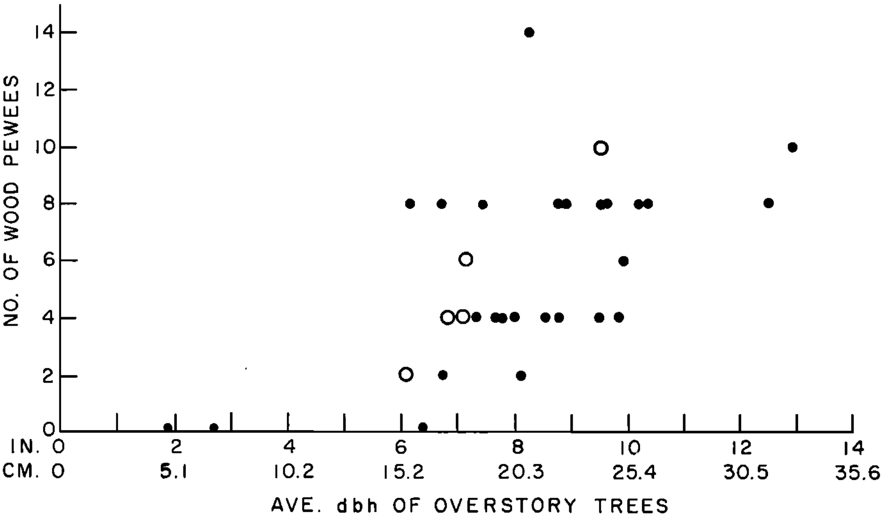


FIGURE 14. The number of Western Wood Pewees in relation to average tree diameter at breast height (dbh).

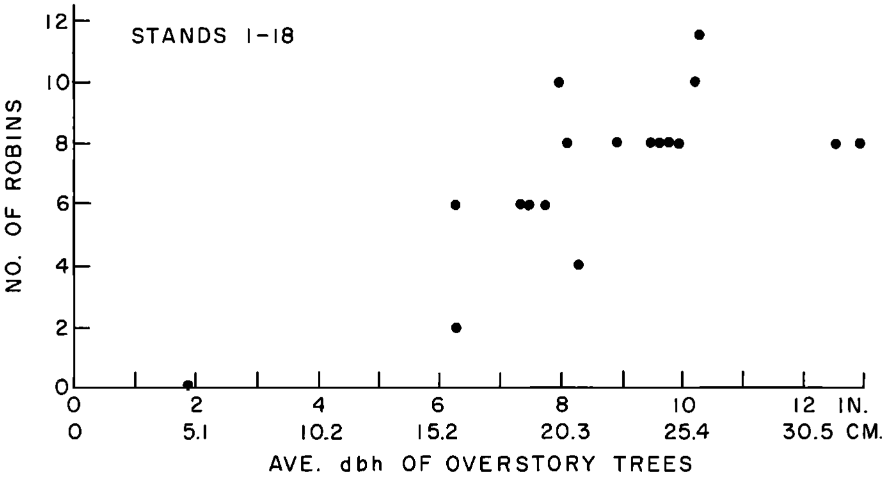


FIGURE 15. The number of American Robins in relation to average tree diameter at breast height (dbh).

In Canada where both the height and thickness of the canopy were correlated with the number of birds nesting in the canopy (guilds 1 + 2), the relationship seems unrelated to limb size, although nest site selection was the same for Robins. The most abundant birds in these groups were

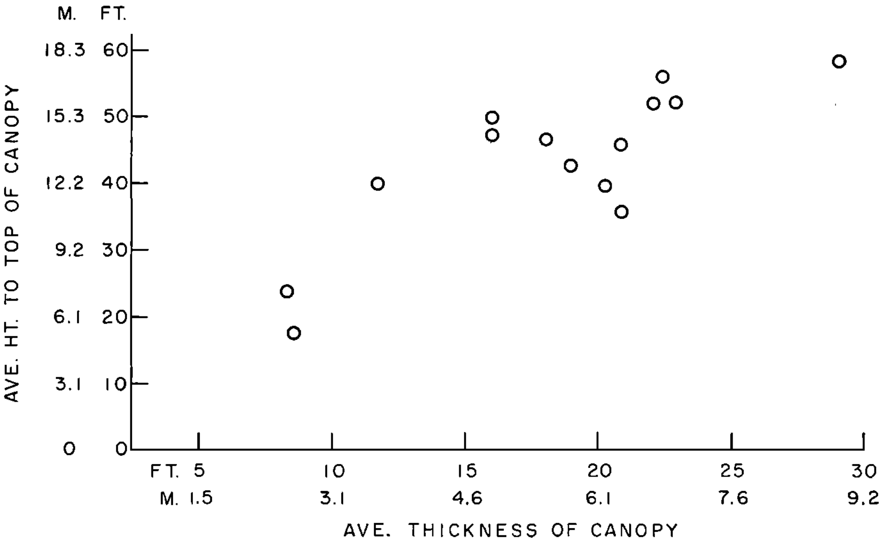


FIGURE 16. The average height to the top of the canopy in relation to the average thickness of the canopy.

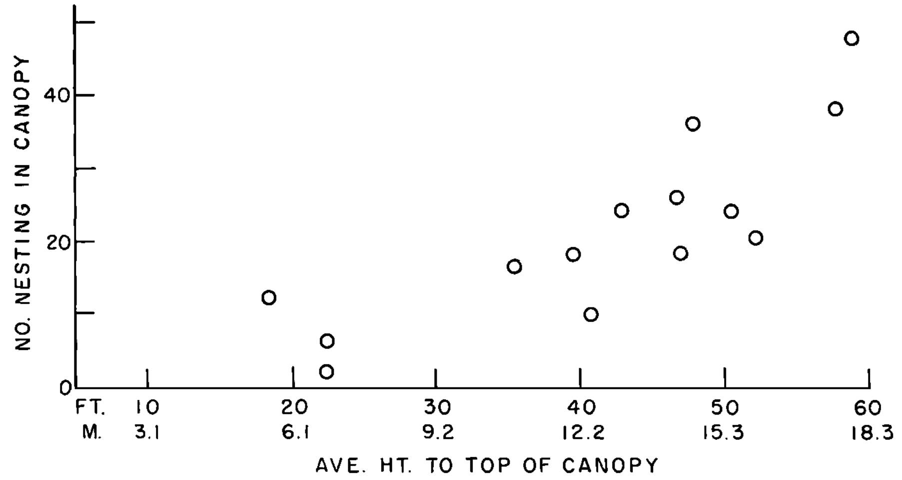


FIGURE 17. The number of birds nesting in the canopy (guilds 1 and 2) in relation to the average height of the canopy.

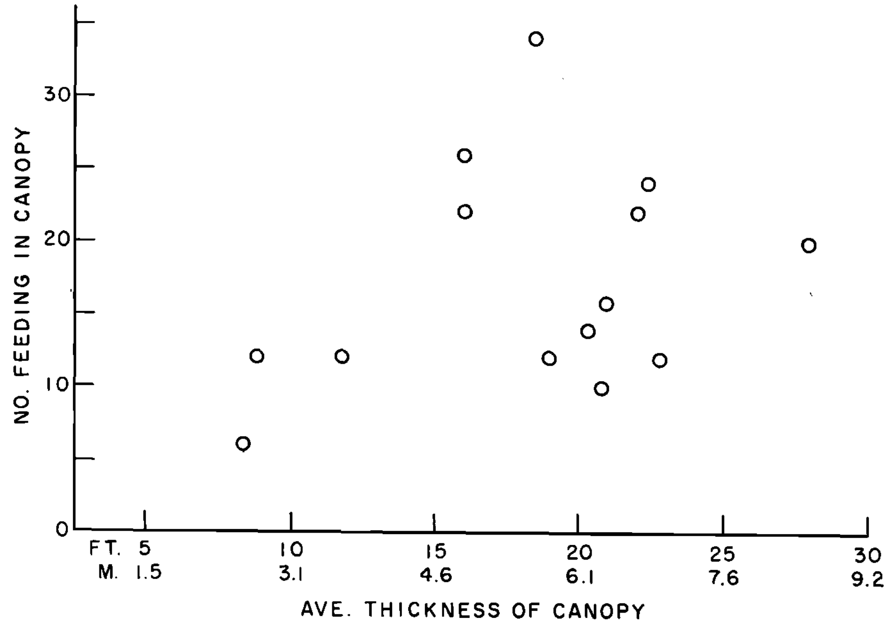


FIGURE 18. The number of birds feeding in the canopy by gleaning (guild 1a) in relation to the average thickness of the canopy.

FIGURE 19. The number of Baltimore Orioles in relation to the average height to the top of the canopy.

not dependent on large limbs but on small peripheral ones for nesting and on foliage for gleaning insects. Since height to the top of the canopy was positively correlated with the thickness of the canopy (Fig. 16), it was not possible to separate the influence of each factor. It seems reasonable however, to assume that the number of nests and foraging sites were related to canopy thickness. Guilds 1 and 2 in the western mountains had a greater abundance of birds than in Canada (Fig. 8 vs Figs. 11 and 17). When species excluded from the summation are considered (Table 1), those guilds were largest in stands 28–30 where representatives of the montane and parkland avifaunas were found, and in stands 32, 35, and 39 where trees were very large. The possible significance of this is considered in the discussion of diversity.

The number of birds feeding by gleaning in the canopy (guild 1a) in stands

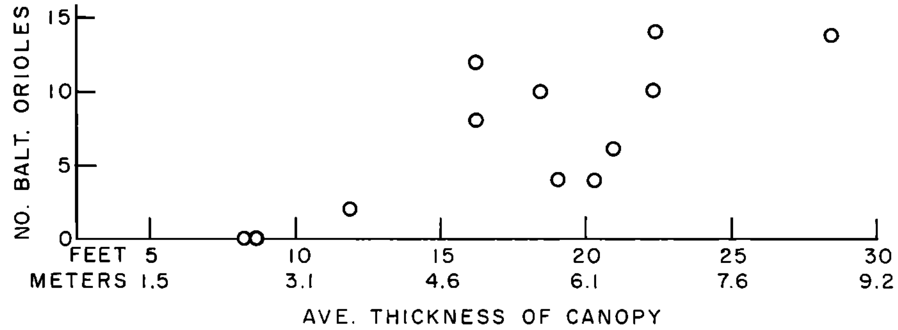


FIGURE 20. The number of Baltimore Orioles in relation to the average thickness of the canopy.

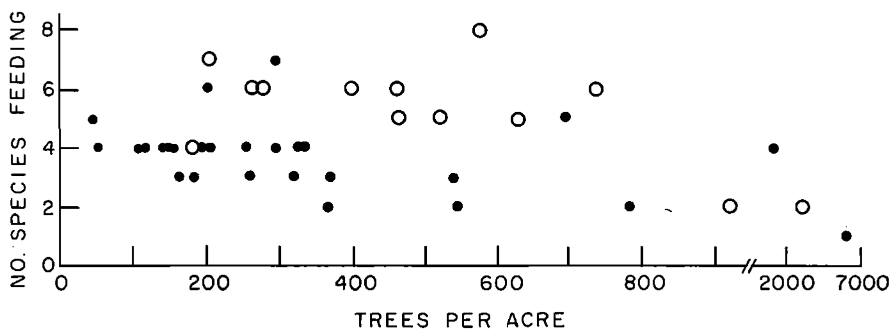


FIGURE 21. The number of species feeding in the canopy (guild 1a) and canopy and shrubs (guild 2a) in relation to tree density.

28–41 increased with greater average thickness of the canopy (Fig. 18) and average height to the top of the canopy (Fig. 17). The number of Baltimore Orioles in a stand shows a very similar relationship to canopy height and thickness (Figs. 19, 20).

The number of species which feed by gleaning in the canopy exclusively (guild 1a), and in the canopy and shrubs (guild 2a), is relatively constant

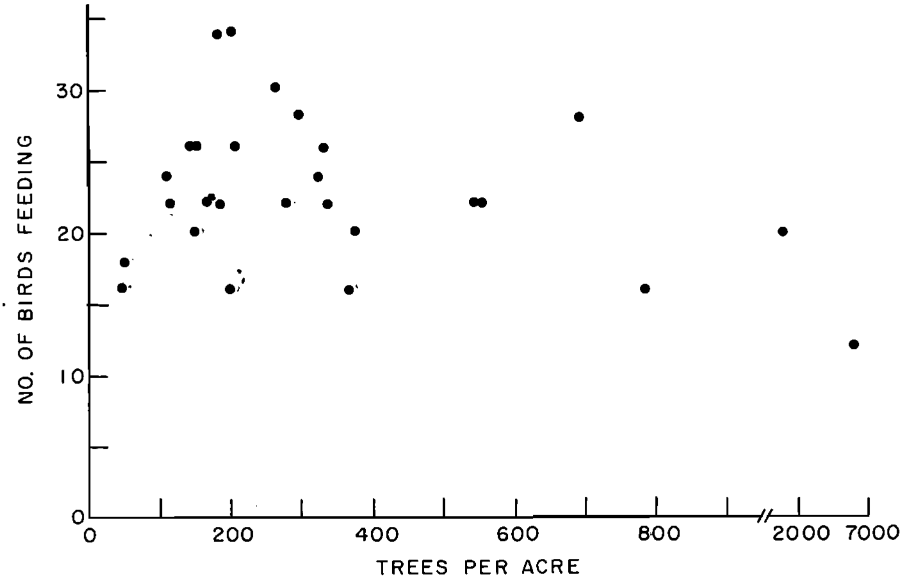


FIGURE 22. The number of birds feeding in the canopy (guild 1a) and canopy and shrubs (guild 2a) in relation to tree density.

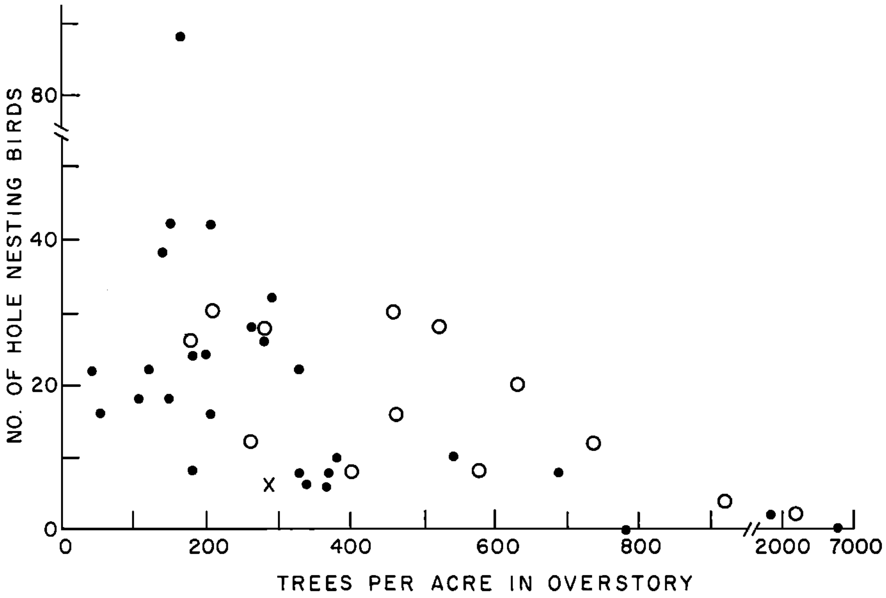


FIGURE 23. The number of hole nesting birds in relation to tree density.

through a wide range of tree densities in both regions, with the Canadian areas having greater numbers of species (Fig. 21). In the western mountains the density of birds in these two feeding guilds increases as tree density increases to 200 per acre and then gradually decreases (Fig. 22).

One would expect the number of birds feeding by gleaning in the canopy

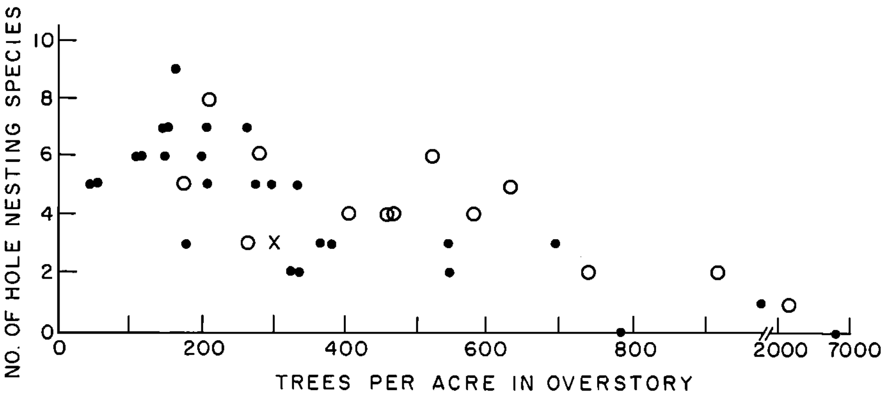


FIGURE 24. The number of hole nesting species in relation to tree density.

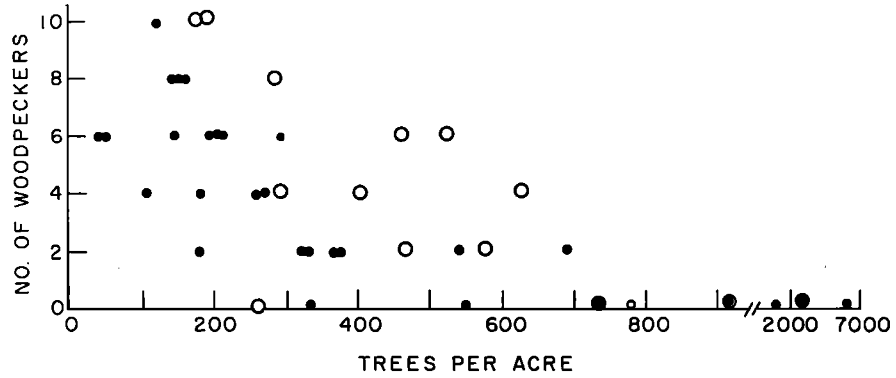


Figure 25. The number of woodpeckers in relation to tree density.

(guild 1a) to be related to the thickness of the canopy, but these birds are much better correlated with the height to the top of the canopy from the ground. Vertical stratification of species niches may be important, particularly for the Baltimore Oriole and Red-eyed Vireo.

The relationship between tree density and the number of birds feeding wholly or partially in the canopy (Figs. 21, 22) suggests that the kinds of niches are rather constant in a forest, but that their abundance is highest in mature forests. It also suggests that the number of kinds of niches is not determined by the habitat alone, but by the factors which gave rise to the

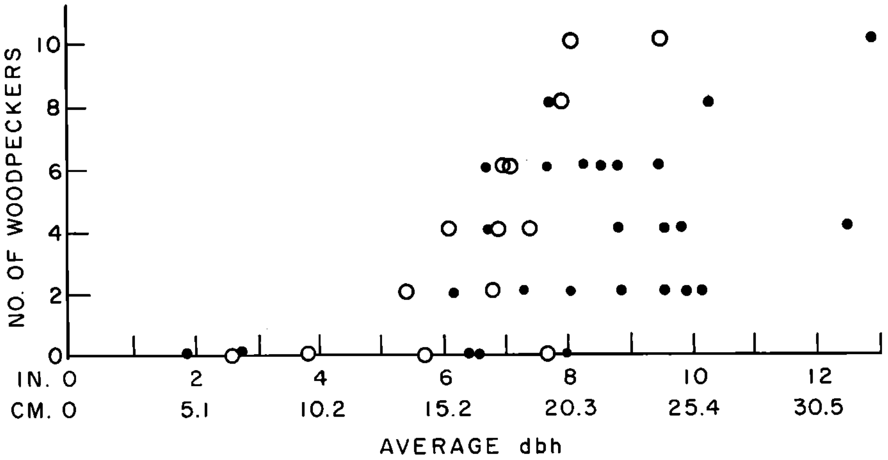


Figure 26. The number of woodpeckers in relation to average tree diameter at breast height (dbh).

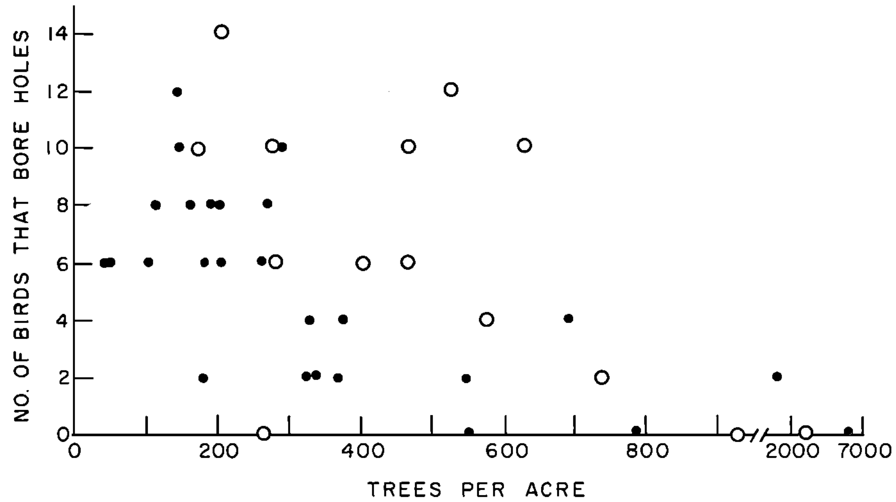


FIGURE 27. The number of birds that excavate holes in relation to tree density.

whole assemblage of birds. For example, the greater number and kinds of birds in these two guilds in Canada may be a result of finer and more efficient division of resources, or a result of a larger number of species available for colonization from eastern deciduous forests that are continuous with the parkland. It also could be correlated with a higher production of insect food in the warmer parkland forests.

CAVITY NESTING BIRDS

The number of birds nesting in holes in stands 1–27 decreased abruptly in stands with tree density greater than 300, while in stands 28–41 in Canada there was a more gradual decrease in numbers of hole nesting birds with increasing tree density (Fig. 23). Highest densities occurred in stands with

TABLE 2
PERCENT FREQUENCY OF OCCURRENCE OF HOLE DIGGING SPECIES

Birds	Mountains	Parkland
Common Flicker	66	29
Pileated Woodpecker		14
Yellow-bellied Sapsucker	26	57
Hairy Woodpecker	22	21
Downy Woodpecker	30	50
Black-capped Chickadee	44	71
Red-breasted Nuthatch		29

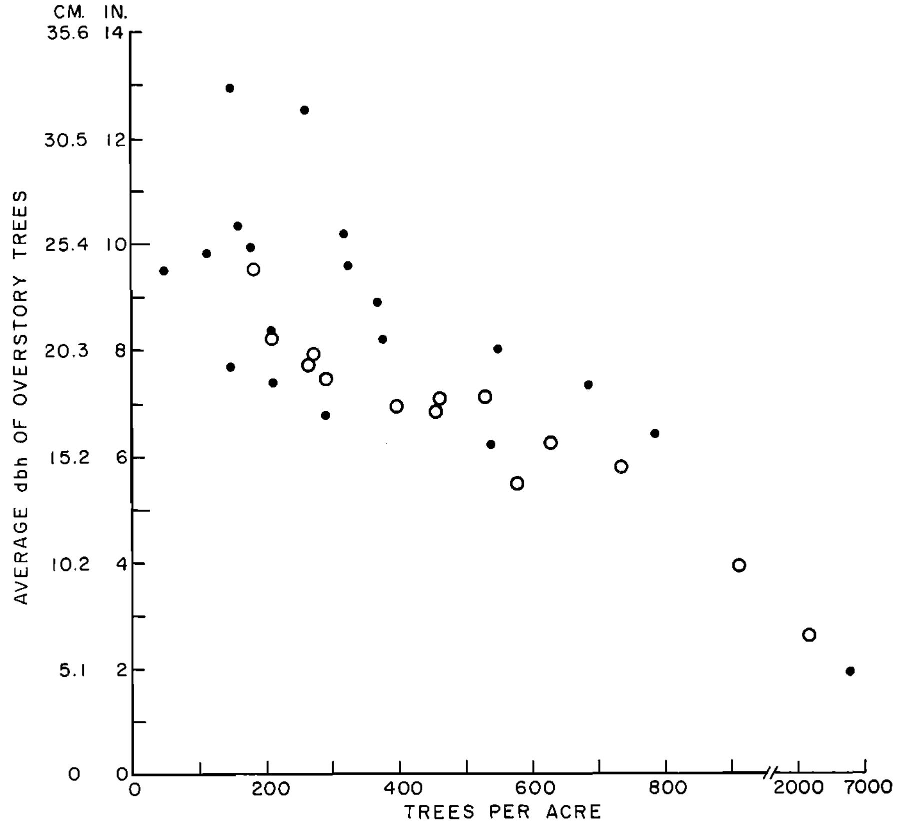


FIGURE 28. Average tree diameter at breast height (dbh) in relation to tree density.

100 to 300 trees per acre. The number of species of hole nesting birds showed a similar difference in the two areas (Fig. 24). The number of woodpeckers also shows this difference between the two regions (Fig. 25). In Figures 23, 24 and 25, 26, 27 one point (stand 40) in addition to stand 34 is consistently low. This appears to be due to three species of woodpeckers having been missed during censusing.

When the number of woodpeckers is plotted against average dbh, their density increases abruptly above six inches dbh in both regions (Fig. 26). In both regions trees do not usually reach this size until density is below 700 per acre (Fig. 28). When all species which excavate holes (woodpeckers, chickadees and nuthatches) are plotted against tree density, the difference between regions is further accentuated (Fig. 27).

The number of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) and Downy Woodpeckers (*Dendrocopos pubescens*) in stands 28–41 increase abruptly

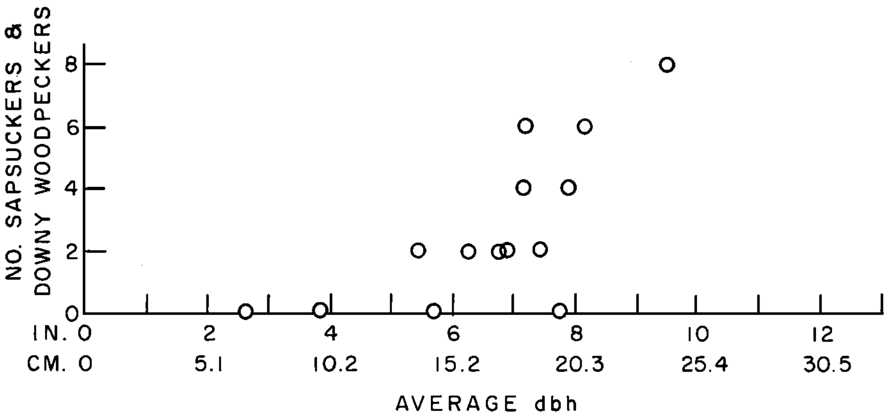


FIGURE 29. The number of sapsuckers and Downy Woodpeckers in relation to average tree diameter at breast height (dbh).

above six inches (15.2 cm) dbh (Fig. 29). A similar relationship exists between all hole nesting birds and dbh, excluding wrens (Fig. 30). Similar patterns in stands 1–27 were not found, where there was much greater variability in the density of hole nesting birds. The number of House Wrens increased roughly with increased average tree dbh (Fig. 31). This species used cavities produced by loose bark, windfalls and woodpeckers.

As the number of excavating hole nesters increased (hereafter: excavators), the number of non-excavating hole nesters (hereafter: cavity dependents) increased in both regions, the increase being more abrupt in stands 1–27 (Fig. 32). A similar relationship can be seen on the basis of species in stands 1–27 (Fig. 33), but not in 28–41. In these latter stands there was an in-

TABLE 3
HEIGHT AND TREE DBH OF NESTS IN HOLES

	No. Nests	Tree Height		Tree dbh	
Birds	No. Nests	range (in feet)	average	range (in inches)	average
Common Flicker	13	8–35	13.2	10–25	15.7
Yellow-bellied Sapsucker	11	3–50	17.5	9–18	12.0
Hairy Woodpecker	6			8–16	11.5
Downy Woodpecker	5			6–12	9.9
Violet-green Swallow	12	12–40	26.9	10–20	13.5
Tree Swallow	29	10–35	20.7	8–25	11.5
Purple Martin	2	15–20	17.5	10–12	11.0
House Wren	12	5–25	12.8	6–20	12.2
Mountain and Western Bluebird	18	3–60	21.7	8–30	13.5

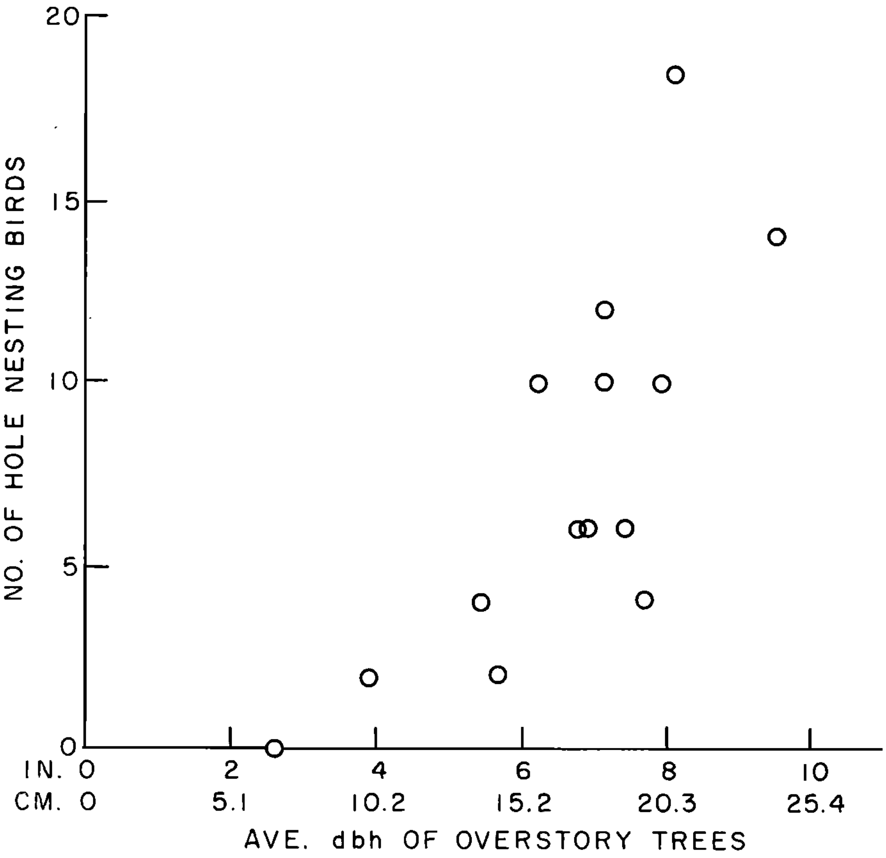


FIGURE 30. The number of hole nesting birds excluding House Wrens in relation to average tree diameter at breast height (dbh).

crease in the numbers of cavity dependent birds as the number of species of hole excavating birds increased (Fig. 34).

It is apparent from Figures 23 through 26 that hole nesting birds colonize aspen forests in Canada when the tree density is higher and dbh typically smaller than in forests in the western mountains. The frequency of the Downy Woodpecker and Yellow-bellied Sapsucker are, moreover, higher in the parkland than the western mountains (Table 2). The Downy Woodpecker may be able to use smaller trees than larger woodpeckers do, as is suggested in Table 3, and the sapsucker frequently excavates live trees (Lawrence 1967). In both regions the density of hole nesting birds is highly variable in mature forests of comparable density. It appears that both phenomena are related to a rather subjective factor in forest structure, the health of the live trees

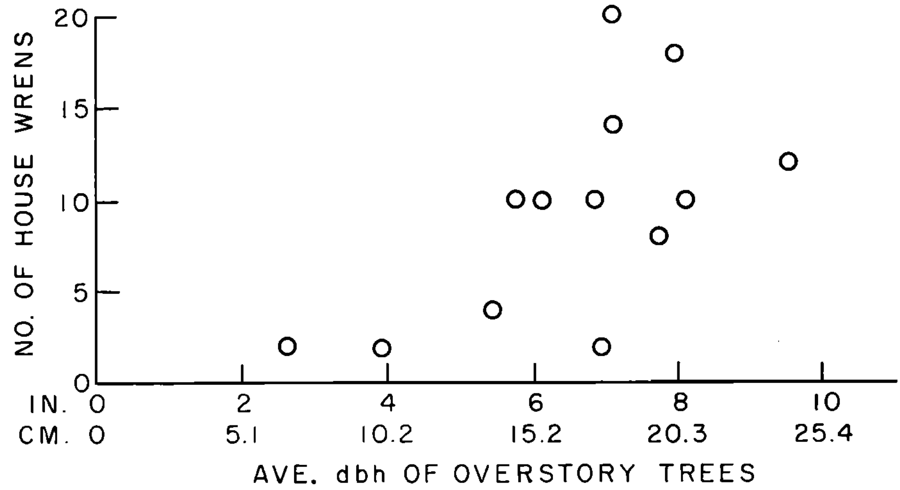


FIGURE 31. The number of House Wrens in relation to average tree diameter at breast height (dbh).

(see Christensen et al. 1951; Bird 1961; Hinds 1964 and Maini and Cayford 1968). This was not realized early enough to make attempts at quantification. Yeager (1955) recorded large increases in woodpecker populations in a hardwood forest after flooding killed the trees.

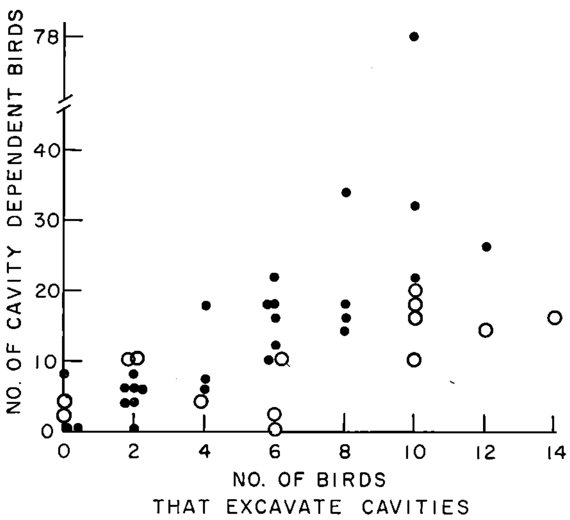


FIGURE 32. The number of cavity dependent birds in relation to the number of birds that excavate cavities.

FIGURE 33. The number of cavity dependent species in relation to the number of species that excavate cavities.

In Canada, it appears that most aspen forests have a life cycle of approximately 65–80 years (Bird 1961; Maini and Cayford 1968: 71) from regeneration to senility, although some live longer. Probably because of the warmer nights and rains during the growing season the trees grow faster, become infected by a number of disease organisms, and die earlier than in the western mountains where trees commonly live 80–100 years, and entire stands frequently survive much longer. Decay is negligible in Utah before 80 or 90 years (Baker 1925). I suggest that selection of aspen forests for purposes of breeding is released by tree dbh (> 6 inches or 15.2 cm) and the general health of the trees. Holes are usually bored in the trunk, infrequently in the

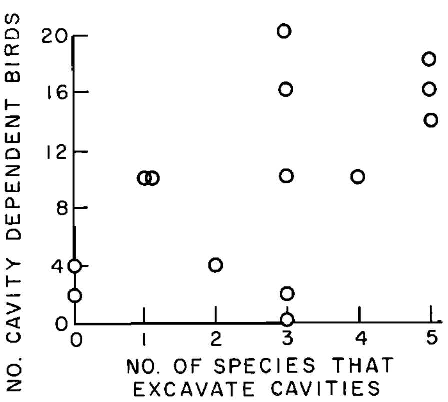


FIGURE 34. The number of cavity dependent birds in relation to the number of species that excavate cavities.

limbs. Haapanen (1965) also notes that only trees of a certain diameter are suitable to birds digging their own holes. I was struck by the lack of disease as indicated by such things as cankers, sap flows and presence of dead limbs, and scars in the mature forest at stands 2 (Arizona) and 8–12 (Colorado), all of which had large trees and low numbers of hole diggers.

In Canada low numbers of hole nesting birds occurred in stands 36 and 40 where trees were uniformly very large and apparently healthy and in stand 34 within the boreal forest. The latter stand had numerous signs of disease.

In addition to differences between stands in tree health, the high degree of variability that cavity dependent species show in stands of 100 to 300 trees per acre or 6–13 inches dbh may in part be a result of the tendency of swallows to nest in aggregates, those stands with more individuals possibly being more attractive than those with few or no individuals present, in spite of nest site availability. In stand 16 where 31 pairs of swallows nested, one pair nested in an abandoned Robin's nest, and three species were found nesting in one tree. In only four out of nineteen occurrences were fewer than three pairs found in one stand. Finally, in stands most favorable to woodpeckers, colonies will have numerous new nest sites each year; in very old forests the total number of such cavities may be very great. Competition among hole nesting birds is severe, and populations become very dense where cavities are abundant (Pfeifer 1963; von Haartman 1957, 1968). Therefore, it is not surprising that there is a correlation between the number of species, or individuals, dependent on cavities, and the number of species or birds that excavate cavities (Figs. 32, 33, 34). Haapanen (1965) has recorded similar correlations in a number of forests in Finland. In both cases migratory species make up the majority of pairs, and it has been shown that this group, rather than resident species, is most severely limited by availability of nest sites (von Haartman 1957, 1968; Haapanen 1965, 1966).

Although stands in the parkland are colonized sooner than in the western mountains by hole nesting birds, in most cases the total number of species and of individuals found in many comparable mature stands is lowest in the parkland. This is due to a conspicuous lack of cavity dependent birds other than House Wrens in the parkland. The maximum number of woodpeckers found in a stand is the same in the two regions (Figs. 25, 26) with frequency of occurrence higher in the parkland for every species except the flickers (Table 2), while chickadees, nuthatches, and House Wrens are also more common than in the western mountains. In stands 1–27 seven cavity dependent species were recorded, four of which occurred frequently in numbers of more than two pairs, in contrast to stands 28–41 where only one such species was common (Table 1). Both the Tree Swallow (*Iridoprocne bicolor*) and the Mountain Bluebird (*Sialia currucoides*), abundant in the mountains, are widely distributed in the parkland, but of the former, three nestings were recorded in fourteen stands and of the latter, none nested. House Wrens were highly successful in competing with Mountain Bluebirds for nest sites, but they most frequently nested at different heights (Table 3) and Mountain Bluebird abundance in the western mountains was not correlated with wren abundance. This absence or scarcity of most cavity dependent birds in the parkland appears to be related to several independent factors: the shorter life history of aspen; the recency of control of prairie fires; the greater instability of forests in the parkland in pre-settlement times due to climatic changes and fire, and in post World War II times with the clearing of large blocks of forest for croplands; and related to the above factors, the apparent recency of invasion by and continued expansion of the ranges of several bird species.

Every year that a tree can survive after reaching roughly six inches dbh increases its chances of being used by a woodpecker for excavation. The longer it stands after excavation, the greater its utility to cavity dependent birds. After one excavation, the probability of a second in the same tree increases (Lawrence 1967). Considering entire forests, assuming a percentage of the trees are attractive to woodpeckers, greater longevity of trees will result in larger aggregations of nest sites. If individual trees attain greater stature, they probably also can harbor several such cavities and attract the larger woodpeckers. Cavity dependent species, once established, may increase their populations with each breeding season as the number of nest sites increases. Philopatry (Welty 1962; Mayr 1963) in cavity nesting birds is probably important (Kendeigh 1941; Allen and Nice 1952; Chapman 1955; Power 1966; Lawrence 1967; von Haartman 1968). A diversity of such species using a stand may also reduce nest parasites.

Short-lived parkland forests may not become established long enough to attract and maintain high bird populations over a large region. The number of individuals that dig holes is higher in Canada in most stands (Fig. 27), but their activities are lost if trees die and fall at an early age. The shallower slope to Figure 32 indicates that for a given unit of digging activity in the parkland, smaller numbers of cavity-dependent birds succeed in nesting. The following arguments lend strength to the above assumptions.

If the above reasoning is acceptable, then any other factors that shorten the life span of forests would drastically reduce populations of cavity dependent birds. As settlers became more numerous, after a period of increased frequency of fires (Moss 1955; Bird 1961), they began reducing the number, size and intensity of prairie fires in 1880–90, and by the early twentieth century fires ceased periodically to burn large blocks of grassland and forest in the parkland (Bird 1961; Raby 1966). If an aspen tree takes thirty to forty years to reach such a size (5–6 inches dbh see Maini and Cayford 1968: 147) and state of health, as to be attractive to a woodpecker, only thirty years has elapsed since most forests in the entire region could bring up populations of cavity nesting birds. Several stands (28, 35, 39) showed the beginnings of such a build-up. This contrasts with the western mountains discussed below where in many stands, colonization has probably had over 100 years to take place, with the advantage of having a source of individuals from older disintegrating stands in the surrounding area. Although there was a period of frequent large fires in the western mountains with the advent of the logger and stockman (Baker 1925), it is evident from the presence of numerous forests pre-dating this period that entire regions were not devastated at this time, probably because of the great discontinuity of the montane forests.

This leads to the third point, that of greater instability of forests in the parkland in pre-settlement times as compared to the western mountains. "The records of early travellers and settlers, however, indicate that there were major fluctuations of forest and grassland before the white man broke the land for agriculture" (Bird 1961). The major wet and dry periods were the cause of these fluctuations that occurred over the whole region. Favorable periods allowed the growth of trees, in some places into forests of big trees (Bird 1961), but it appears that very few if any areas retained patches large enough to maintain extensive populations of cavity dependent birds during periods when drought and fire destroyed much of the forest. Maini's (1960) conclusions conflict with those of many earlier workers concerning the magnitude of the effect of fire in limiting the invasion of trees into grassland. The point important to this study, however, is concerned with devastation of forests by fires at frequent intervals wherever they developed, especially near the northern edge of the parkland. Farming practices in the last decade, especially in Saskatchewan and Alberta, have further resulted in the clearing of enormous areas of mature aspen forest (Bird 1961; Kabzems 1959, and personal observation), introducing further instability to the developing habitat and its birds.

In contrast, there is abundant evidence that during this same period cataclysmic events of a similar nature did not occur simultaneously or as frequently to the aspen forests of the western mountains (Fetherolf 1917; Baker 1918, 1921, 1925; Daubenmire 1943; Reed 1952; Langenheim 1962; Ream 1963). In recent times fires have been neither frequent nor large. However, serious disturbance of cavity nesting birds may result if the recently begun lumbering operations in aspen forests in the southern Rocky Mountains include cutting of old growth forests. The great age of individual stands of trees within a mosiac pattern of forests of many different ages in a region of the western mountains provides the habitat to maintain populations of cavity nesting birds at high levels indefinitely, without disasterous crashes due to loss of habitat.

It may be legitimately contended that since entire populations of cavity dependent birds are adversely affected by habitat instability, woodpecker populations should also be periodically decimated. Two important differences between these groups of birds may account for the more rapid recovery of woodpeckers. In the first place, woodpeckers are able to excavate new nest cavities each year and most usually do so (Hoyt 1957; Lawrence 1967), and therefore could both relocate territories more easily and invade young forests sooner than cavity dependent birds. Since settlement and especially since rural electrification in the parkland, utility poles have been used by flickers, bluebirds and other species (Bird, 1961) and such factors may have had a stabilizing influence. Increased usage of creosote on these poles may reverse this effect (Rumsey 1970). Probably also of importance is the proximity of the mixed boreal forest, in which fire favors aspen over spruce (Hansen 1949), which was subject to less frequent large fires in presettlement times than the parkland (La Roi 1967), and from which woodpeckers could move south. Most birds of the cavity dependent group appear to be less common in the mixed boreal forest (see Salt and Wilk 1966; Houston and Street, 1959). The House Wren's success is probably related to other factors such as the variety of acceptable nest sites and habitats to which it is adapted. In addition to the direct evidence of low populations of cavity dependent birds (Table 1), the recency of invasion and the continued range expansion of several species of parkland birds supports the above hypothesis of habitat instability.

The Mountain Bluebird was recorded in central Saskatchewan (Prince Albert) in 1898 but it seems not to have become common in the southern mixed boreal forest region and parkland until the 1930's (Houston and Street 1959). Its range has since overlapped with that of the Eastern Bluebird with which it is interfertile (Lane 1968). Although widespread, it does not appear to have become as numerous as in the western mountains, where as many as 4 pairs have nested in less than 20 acres of forest. The recent clearing of parkland forest combined with the invasion of the Starling (*Sturnus vulgaris*) into the region (Myres 1958) are two factors that may have contributed to this bluebirds' recent decline in numbers, but other factors may be the cause (Power, 1966).

Tree Swallows, which nest throughout the boreal and parkland regions nested in 2 out of 14 stands as compared to 10 out of 20 stands within its range in the mountains. The Great Crested Flycatcher (*Myiarchus crinitus*) appears to be continuing to expand its range northwestward in Saskatchewan (Houston and Street 1959). This cavity nesting bird was relatively common only in the area of Good Spirit Lake, Saskatchewan, where extensive old growth forests exist. Starlings, although commonly seen, were not recorded nesting in any stand, despite the success of their recent invasion. Many

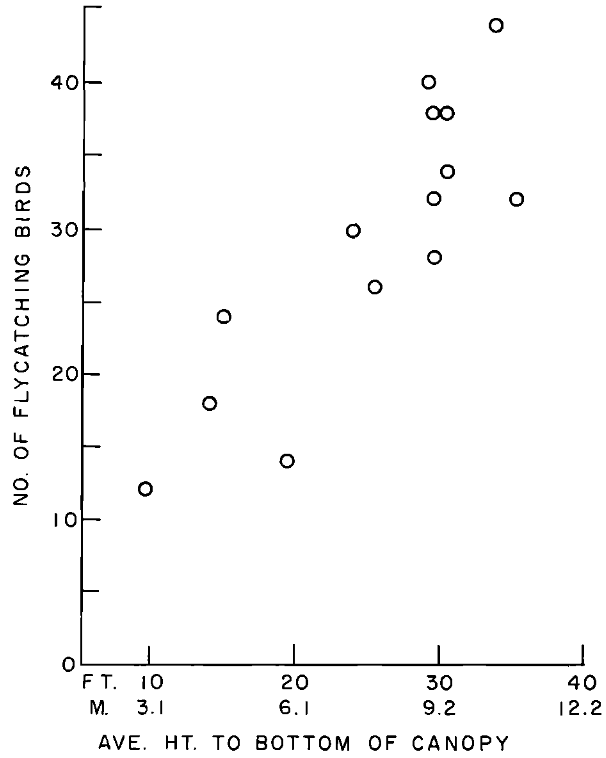


FIGURE 35. The number of birds that feed by flycatching in relation to the average height to the bottom of the canopy.

stands were closely associated with barnyards and houses. Two other birds preferring large trees for nesting are the Baltimore Oriole and Western Wood Pewee (Figs. 13, 14, 19, 20). This pewee was one of the most common birds in the western mountains (89% of 27 stands), but was, by comparison, uncommon in the parkland (44% of 14 stands). It is considered common in parts of the mixed boreal forest (Houston and Street 1959). It is possible that this difference is related to other factors, such as interactions with Least Flycatchers, but its abundance in stand 35 where the trees were very large and flycatchers abundant suggests habitat structure is of key importance. Baltimore Orioles may have extended their range and increased their abundance in parts of the parkland (Bird 1961), especially in Alberta, since settlement, although this is poorly documented (pers. comm. W. Ray Salt 1970), suggesting again that the preferred habitat, mature forest, has become widespread in the parkland only since settlement. Both these species may be expected to invade a forest sooner and become abundant faster than cavity nesting birds, which is the case.

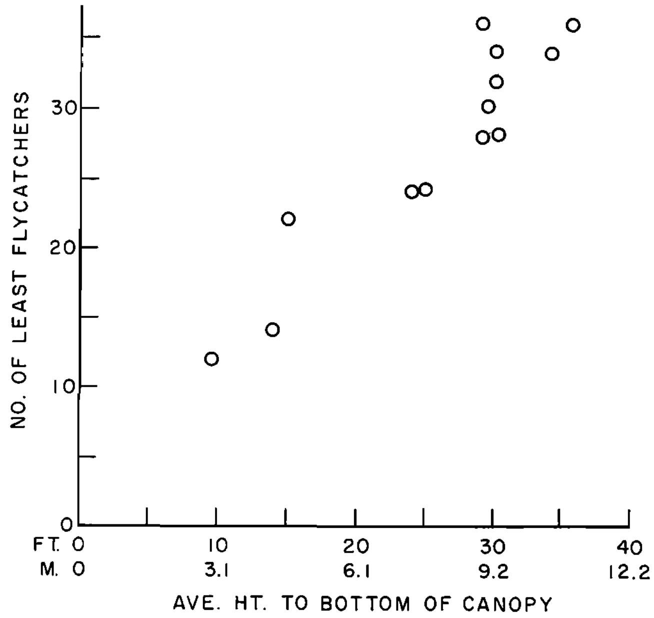


FIGURE 36. The number of Least Flycatchers in relation to the average height to the bottom of the canopy.

In summary, a large number of bird species in aspen forests are dependent on tree size and health, and on the longevity of forests over a large area. This partly explains the high bird species diversity of a habitat that on the basis of its other features, such as foliage diversity or potential successional position, may not be expected to be so diverse (see Tramer 1968). Aspen further seems to be more attractive to hole digging species than most other deciduous and coniferous species. Lawrence (1967) discusses this in more detail. Haapanen (1966) demonstrates this in Finnish forests for *Populus tremula*.

FLYCATCHING BIRDS

The number of birds feeding by flycatching increases with increased average height to the bottom of the canopy (Fig. 35). The number of Least Flycatchers in Canada had a similar relationship to distance between the ground and bottom of the canopy (Fig. 36) and was also roughly correlated with increased dbh and decreased tree density. In these stands average height to the bottom of the canopy was roughly correlated with tree density (Fig. 37). Stand 28 was located near the upper altitudinal limits of the parkland and the forest was composed of old trees of large dbh but short stature. The density

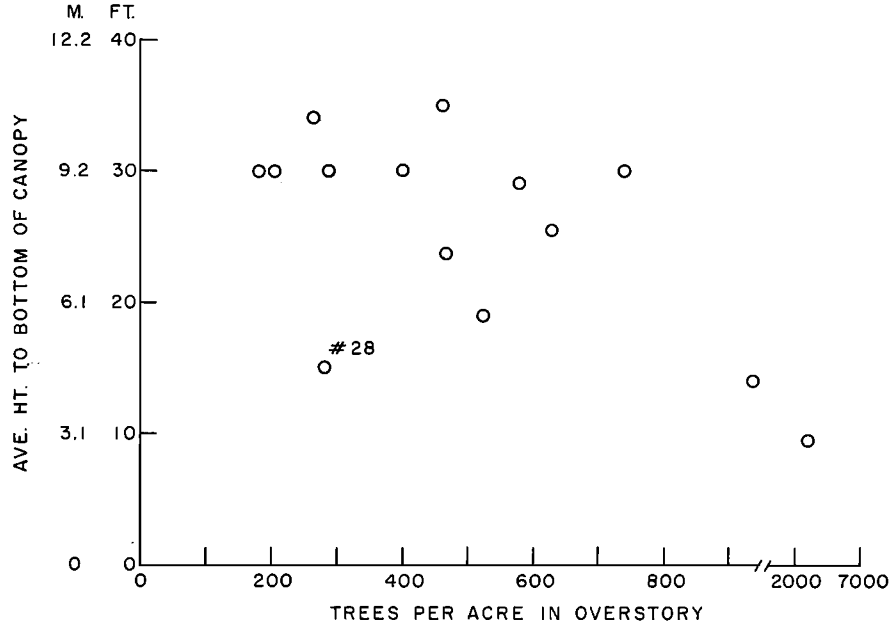


FIGURE 37. The average height to the bottom of the canopy in relation to tree density. Stand 28 was located near the upper altitudinal limit of parkland aspen and the trees were stunted in height only.

of flycatching birds decreased as tree density increased, numbers being much higher in Canadian stands (Fig. 38), although there were generally more species found in stands in the western mountains (Fig. 39). The low number of flycatching birds in stand 29 was possibly related to the relatively high density of large, short (somewhat stunted as in stand 28) trees.

Breckenridge (1956) found that the abundance of the Least Flycatcher was correlated with the degree of openness beneath the crowns of the forest canopy. If openness is mainly a function of height to the bottom of the canopy, then it can be seen that her findings are applicable to all flycatching birds (Fig. 35) and also to Least Flycatchers in Canada (Fig. 36). Other factors may, however, influence openness, and the effect of tree density on flycatching birds in the two regions is similar (Fig. 38). In Canada, height to the bottom of the canopy was only roughly correlated with tree density. That openness may not have been the only major factor operating in the western mountains is suggested by the dependence of Western Wood Pewees and bluebirds on mature forests for nest sites. The greater number of flycatching birds in Canada was the result of high densities of Least Flycatchers. The total number of species of flycatching birds found in stands in Canada

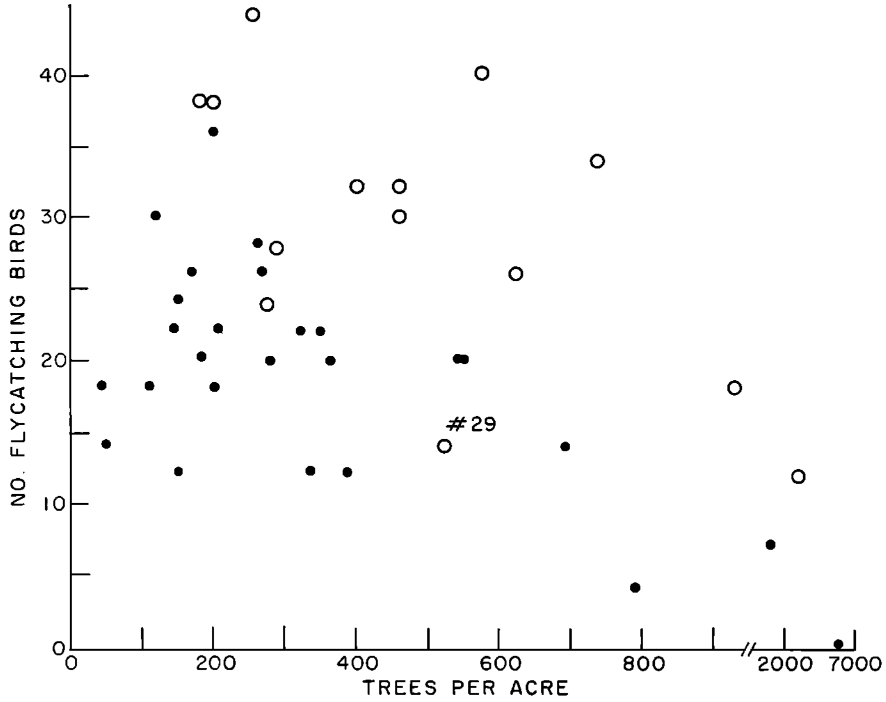


FIGURE 38. The number of flycatching birds in relation to tree density. Stand 29 is discussed in the text.

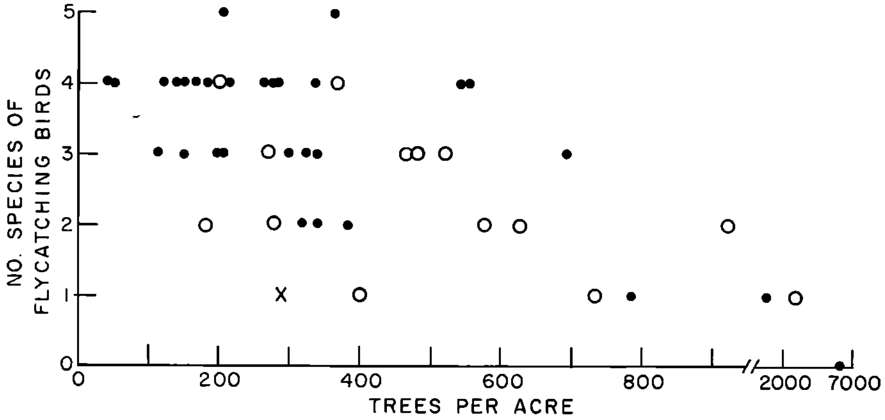


FIGURE 39. The number of species of flycatching birds in relation to tree density.

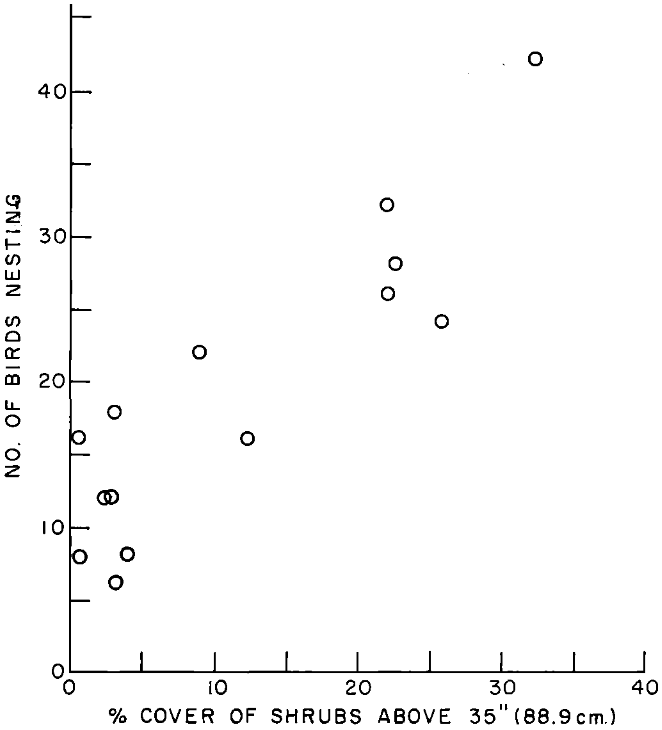


FIGURE 40. The number of birds nesting in shrubs in relation to the percent cover of shrubs above 35 inches (88.9 cm).

was nearly twice that in the western mountains (Table 1), but the number of species per stand, if an average is used, was lower in Canada. This may be due to some competitive factor between the abundant Least Flycatcher and other flycatching birds or the result of historically rooted habitat differences. The latter seems more likely, because the Mountain Bluebird and Western Wood Pewee, both important flycatching birds in the western mountains, and the Great Crested Flycatcher have possibly not reached maximum numbers in the parkland for reasons already discussed. An additional factor, not evident in the data discussed, is the scarcity of *Empidonax* flycatchers in the southern Rocky Mountains (Table 1). Their numbers in that region show no relation to structural features of the habitat. The dry virtually shrubless forests may be unsuitable to larger populations.

SHRUB AND GROUND NESTING BIRDS

The number of birds nesting in shrubs increased as the percent cover of shrubs above 35 inches (88.9 cm) increased in stands 28–41 (Fig. 40). The

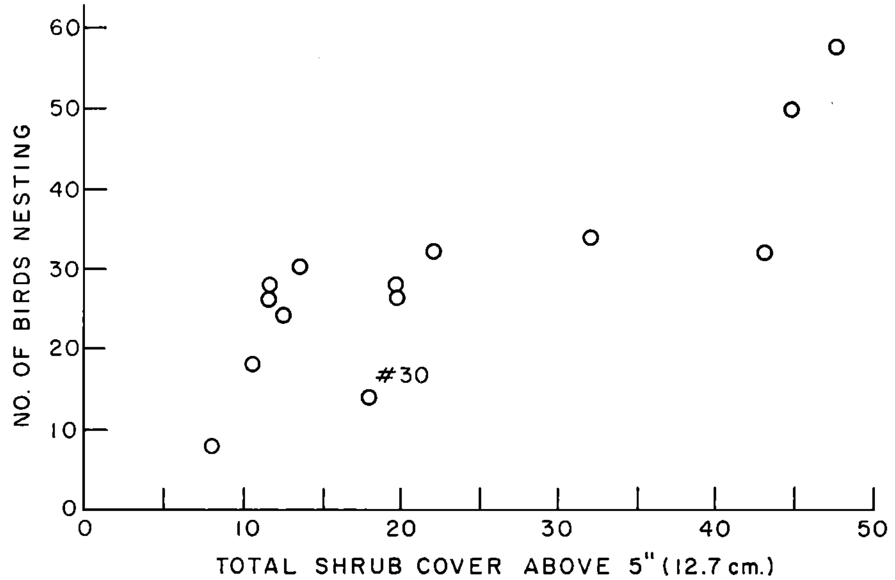


FIGURE 41. The number of birds nesting on the ground and in shrubs in relation to the total shrub cover above 5 inches (12.7 cm).

number of birds nesting on the ground and in shrubs (guilds 3 and 5) increased as total shrub cover increased in stands 28–41 (Fig. 41). The number of birds that feed in both the shrubs and canopy (guild 2b) increased as total shrub cover above five inches (12.7 cm) increased in these stands (Fig. 42).

The synthetic understory cover value referred to below is the sum of the total percent cover of shrubs × 10 plus percent cover of grasses and forbs. In both regions the number of birds nesting in shrubs increased as the understory cover value increased (Fig. 43). A similar pattern is found for the combined number of birds nesting in shrubs and on the ground (Fig. 44).

Outside of Wyoming only four stands in the western mountains show shrub cover values greater than 1%. Stands in southern Utah, southwestern Colorado, Arizona, and New Mexico (except stand 7 with an unusual shrub layer of 1.8% *Juniperus*), had shrub cover values of 0 to 0.9%. It is surprising that shrub nesting species were present in these stands. Birds located their nests on small trees, saplings, small conifers and the occasional shrub. In Wyoming, Yellow Warblers and shrub nesting *Empidonax* flycatchers were abundant.

The varied assemblage of birds found in shrubs have a diversity of foraging requirements and methods for which correlations with the vegetation were

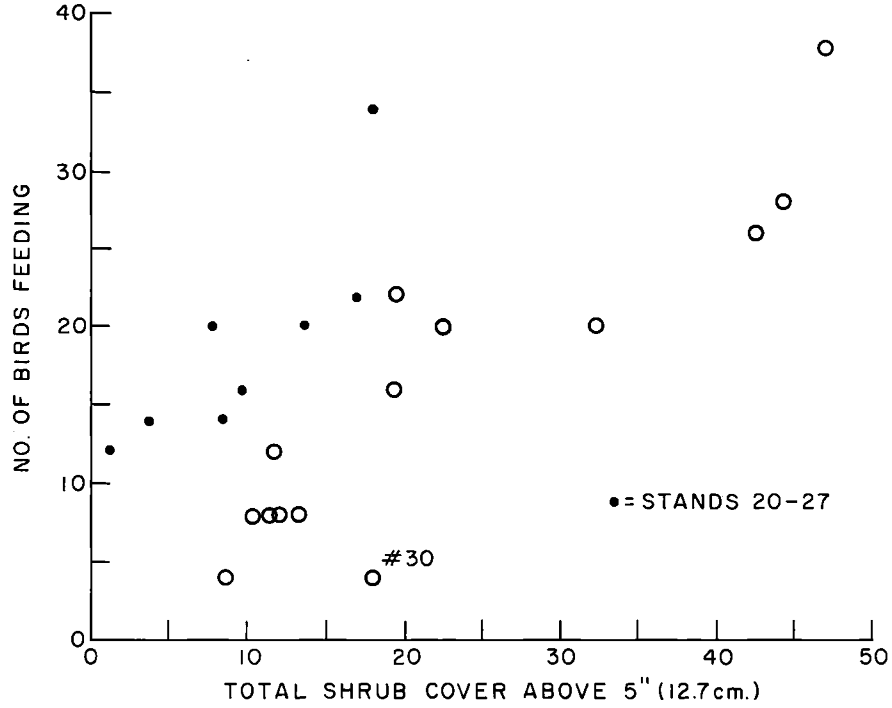


FIGURE 42. The number of birds that feed in both shrubs and canopy (guild 2a) in relation to total shrub cover above 5 inches (12.7 cm).

not found. The positive relationship between the number of birds feeding in both the shrubs and canopy (guild 2a, Fig. 42) and total shrub cover was not surprising since the two important representatives, the grosbeaks and the Yellow Warbler, both of which partially use the canopy, were correlated with total amount of shrub cover (Figs. 45, 46, 47). In the former species one point, stand 19, fell out of place. This stand had few shrubs but averaged 11 feet to the bottom of the canopy. The Yellow Warblers response to shrub cover was modified by the apparent necessity of having surface water nearby. Stand 41 was located roughly 300 yards from the nearest pool of water, and it did not fit the graph.

The correlation between shrub nesting birds and total understory cover suggested that the actual cover was important to the birds, and not the kinds of material or their physiognomy. With respect to this, however, the shrubs and canopy of stand 32 were more than 75% defoliated by caterpillars on June 10, a process which began with leafing-out, but no changes in bird den-

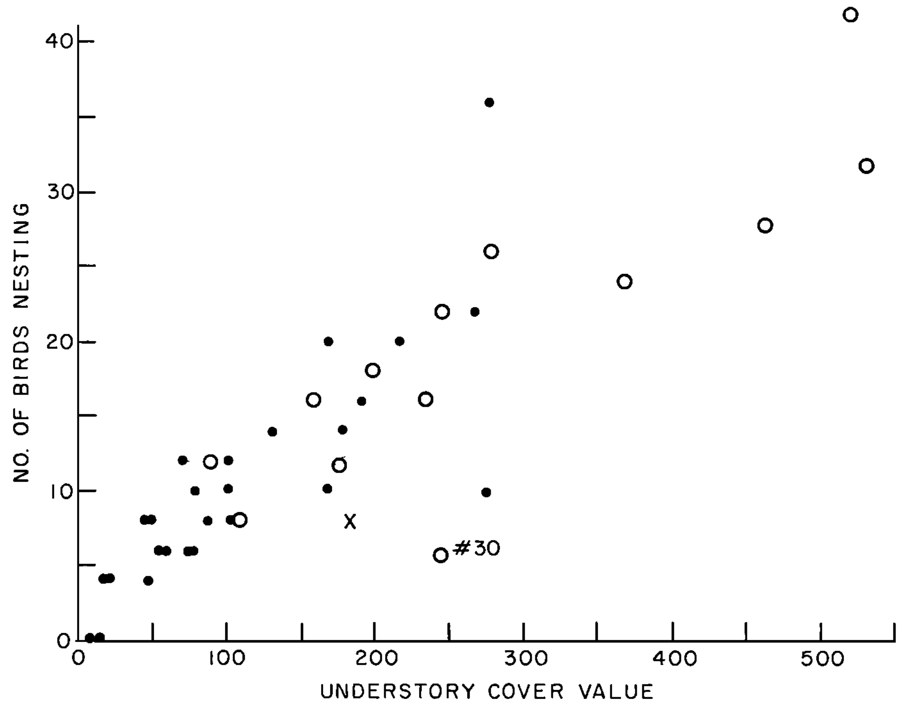


FIGURE 43. The number of birds nesting in shrubs in relation to the understory cover value. Understory cover value is defined on p. 48.

sity were noted. Leaves were well regenerated three weeks later. Fashingbauer et al. (1957) recorded a similar lack of influence of caterpillar defoliation in Minnesota. In Canada a good correlation between shrub nesting birds and shrub cover could be obtained only when shrubs taller than 35 inches (88.9 cm) were considered. Below 35 inches grasses and forbs are probably visually continuous with shrubs. That this is probable is shown in the composite index of all cover (Fig. 43) where densities of shrub nesting birds in stands with low amounts of shrub cover are correlated with herbaceous cover. Since a nest needs only a few well placed twigs, the total number of them is unimportant, but how well they are concealed is paramount. It is also probable that the arrangement of the shrub mosiac, or the patchiness (MacArthur 1964), is important, but this was not measured. When the birds that nested in shrubs and on the ground (guilds 2 and 5) are lumped and plotted against cover (Figs. 41, 44), the patterns are very similar to that for shrub nesting birds alone (Figs. 40, 43), except that shrub cover from the ground up instead of only above 35 inches (88.9 cm) was of importance.

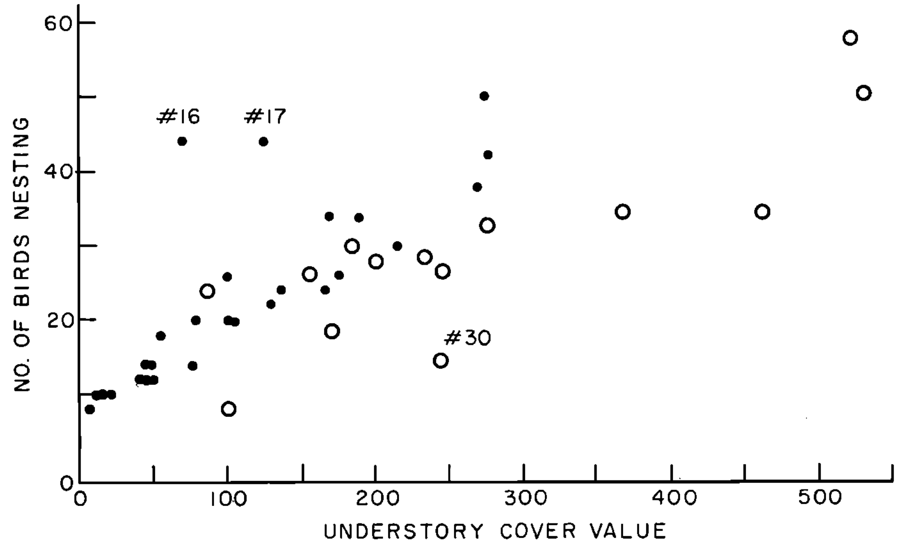


FIGURE 44. The number of birds nesting in the shrubs and on the ground in relation to the understory cover value. Stands 16, 17 and 30 are discussed in the text.

Points from stands 16 and 17 do not fit this graph. Their high densities were the result of large aggregations of White-crowned Sparrows (*Zonotrichia leucophrys*).

In Figures 43 and 44 it is evident that abundance values for shrub and for shrub and ground nesting birds were very similar in the two regions. However, there were more species of birds nesting in shrubs and on the ground in the parkland than in the mountains and there were more common species in the parkland than the mountain guilds (Table 1).

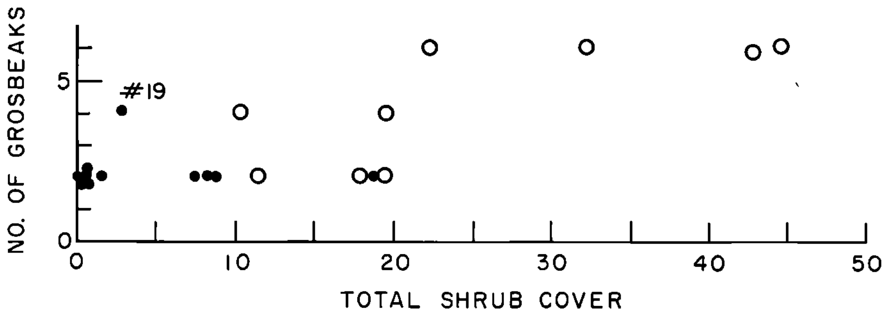


FIGURE 45. The number of grosbeaks (*Pheucticus ludovicianus* and *P. melanocephalus*) in relation to total shrub cover. Stand 19 lacked much shrub cover, but the trees were extremely stunted in height. The grosbeaks nested in the trees.

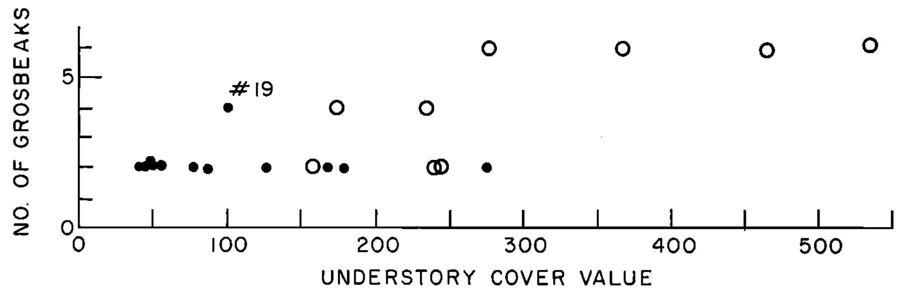


FIGURE 46. The number of grosbeaks in relation to the understory cover value.

Stand 30 is not consistent with these findings, showing low values for shrub and ground nesting birds. The geographic location of this stand is just north of the range of the White-crowned Sparrow and, Black-headed Grosbeak and just south of the range of the Rose-breasted Grosbeak, White-throated Sparrow, American Redstart, and Connecticut Warbler (Salt and Wilk 1966) and on the edge of the range of the Hermit Thrush (Dilger 1956) and the Ovenbird. These absences were not compensated for by the invasion of birds from other habitats, the only adjoining and nearby habitats being hay meadow and short grass prairie. This penomenon would seem to have a mainly historical explanation, discussed in a later section.

Ground nesting birds, when considered by themselves, did not show any correlations with shrub cover. This does not mean that other features of shrub cover are not important to ground nesting birds. Lowther (*in* Bent 1968) has shown that the White-throated Sparrow, a ground nester, selects nest

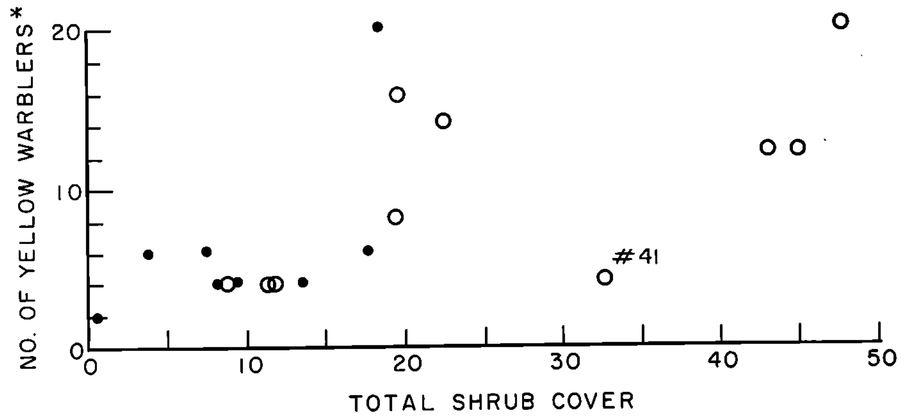


FIGURE 47. The number of Yellow Warblers in relation to total shrub cover. *Only stands with pools of surface water nearby are included, except stand 41.

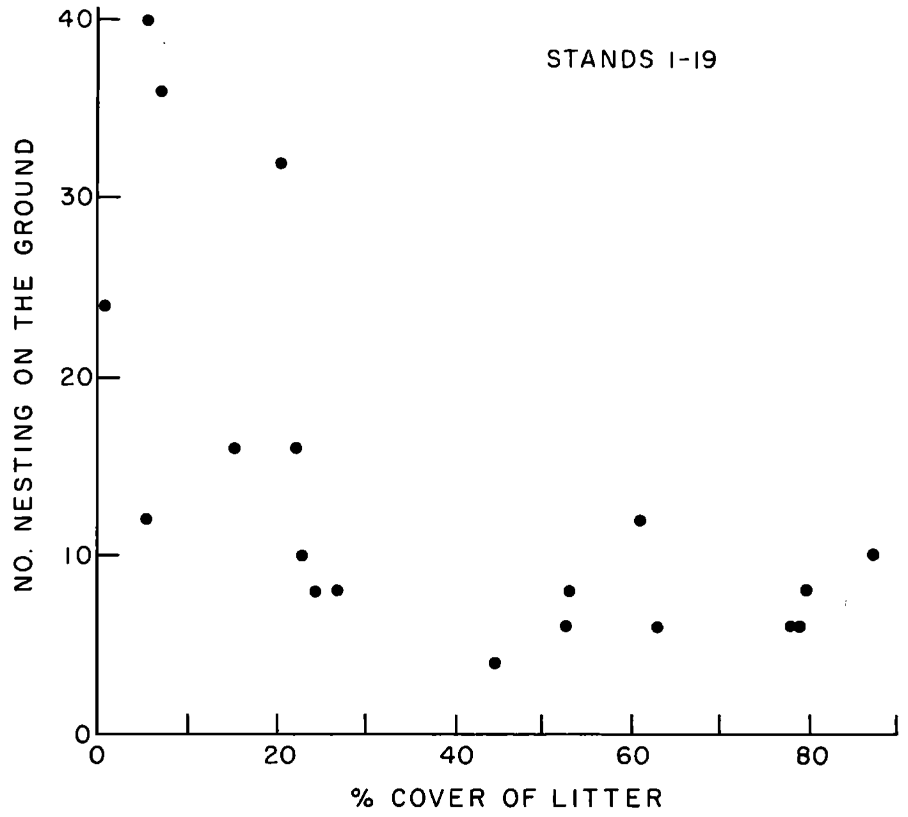


FIGURE 48. The number of birds nesting on the ground in relation to percent cover of litter.

sites in relation to "the amount and dispersion of the nearby cover" that includes shrubs.

In the western mountains, the number of birds nesting on the ground dropped as percent cover of litter increased (Fig. 48). In Canada the number of birds nesting on the ground only could not be related to any of the vegetational parameters measured, although no high densities of such birds occurred in stands with low forb cover, and no low bird densities occurred in stands with high forb cover.

The number of species feeding on the ground in stands 1–19 was relatively constant through a wide range of tree densities, decreasing somewhat in the most dense forests (Fig. 49). The number of birds feeding on the ground in both regions dropped rapidly as the percent cover of litter increased (Fig. 50). The number of birds feeding on the ground in Canada increased as the percent

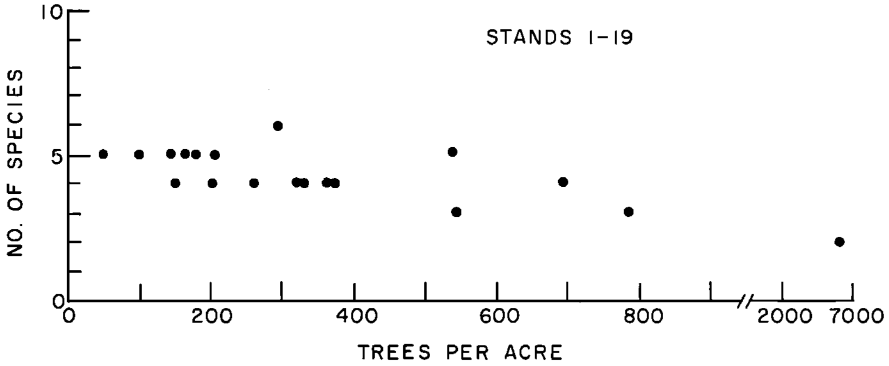


FIGURE 49. The number of species feeding on the ground in relation to tree density

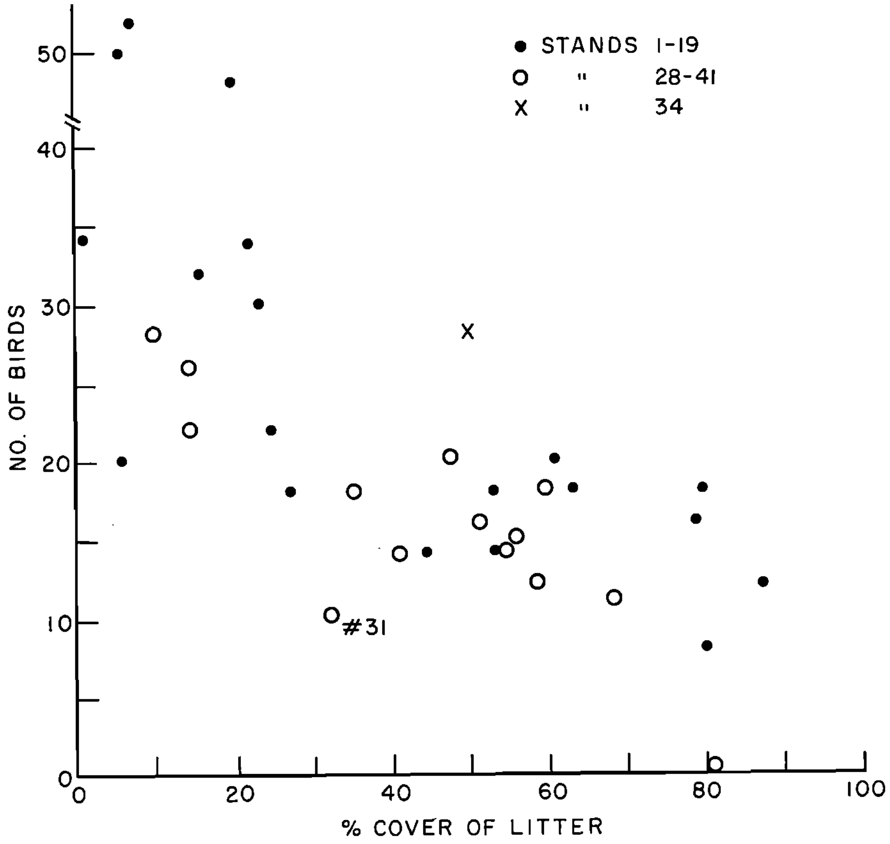


FIGURE 50. The number of birds feeding on the ground in relation to the percent cover of litter. Stand 31 is discussed in the text.

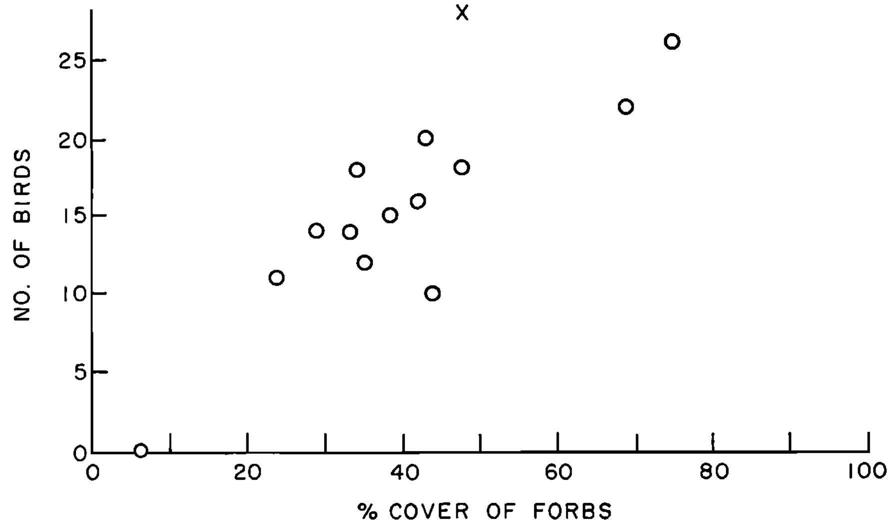


FIGURE 51. The number of birds feeding on the ground in relation to the percent cover of forbs.

cover of forbs increased (Fig. 51). Values for stand 34 in these two figures are high while in stand 31 values are low. It appears that the high value is related to the more favorable conditions for Ovenbirds in the boreal forest, and the low value is related to the position of the stand near the southern edge of the range of the Ovenbird.

Ground nesting birds in Canada or Wyoming showed no correlations with herbaceous vegetation or litter, whereas in the remaining area where shrubs

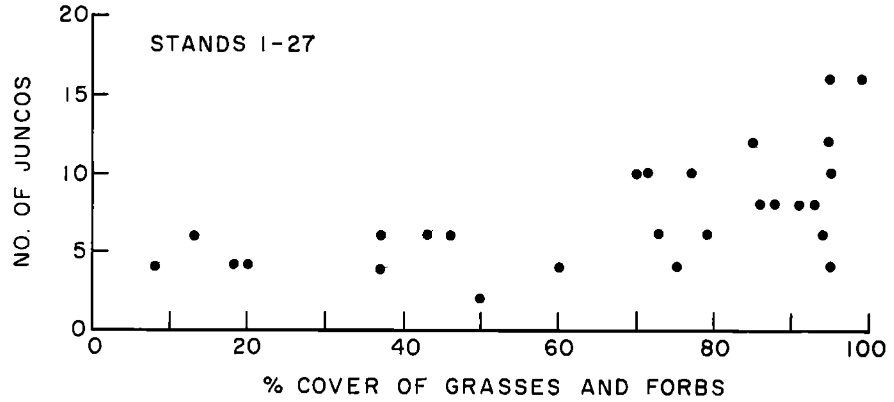


FIGURE 52. The number of juncos in relation to percent cover of grasses and forbs.

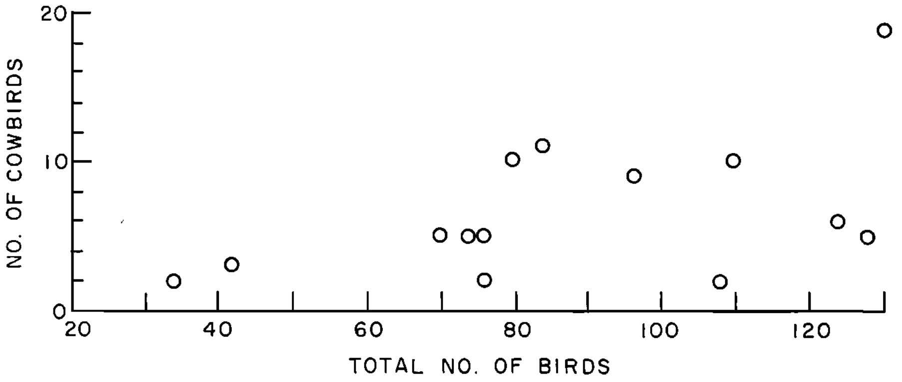


FIGURE 53. The number of Brown-headed Cowbirds in relation to the total number of birds in the summations.

were important in only four stands, ground nesting birds were correlated negatively with the amount of litter on the forest floor (Fig. 48). This supports assumptions about the combined influence of shrubs and herbaceous vegetation when they are both present. The amount of litter in most stands is a measure of the openness of the forest floor, except that in stands with large amounts of bare mineral earth, litter underestimates openness. Thus the total herbaceous cover (grasses and forbs) is a better estimate of ground cover. The juncos appear to favor stands with dense herbaceous cover (Fig. 52) for location of nests that are invariably concealed in dense clumps of vegatation. Seven of eight nests were located under clumps of grass, but abundance was not correlated with grass cover except in stands 20–27. Few of the nests found were located in stands with very dense ground cover where the species was most abundant. Most stands were dominated by either grasses or forbs but it seemed that the junco selected its habitat on the basis of cover value rather than type.

The assemblage of birds that feed on the ground includes species from four of the five nesting guilds. Nevertheless, in both regions, densities were correlated negatively with the amount of litter. Densities were comparable in the two regions, with the exception of the three stands where large colonies of White-crowned Sparrows nested. In Canada this guild was also positively correlated with percent cover of forbs.

When the birds arrive in May, herbaceous ground cover is greatly reduced and shrubs are often leafless. In stands where grass and large forbs are important, I have observed that this reduction of cover over the winter is much less than in stands with low grass and forb cover values. The birds may respond to such proximate features. Others may be returning to the stand

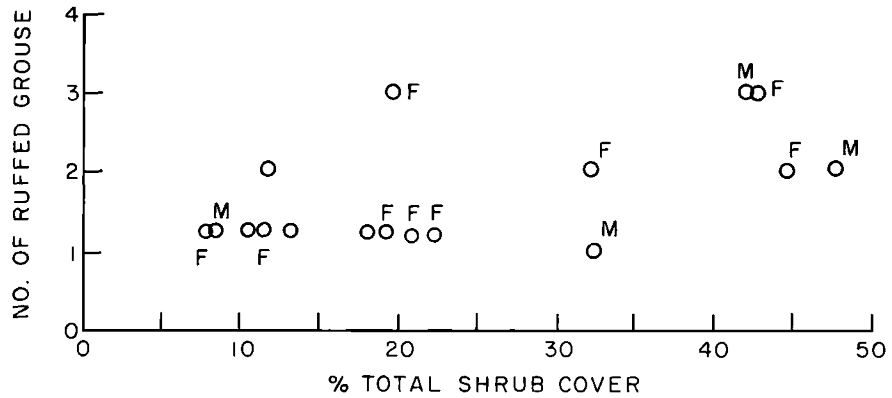


FIGURE 54. The number of Ruffed Grouse in relation to the total shrub cover. Males (M) and females (F) are distinguished.

where they were fledged or had bred previously, and not respond at all to the state of vegetation in spring.

During late May and the first half of June, Brown-headed Cowbirds were a very noticeable element in most forests in Canada, but seemed much less abundant in the western mountains. They were most abundant in stand 35 where a small herd of bison was commonly encountered. They occurred in small groups, but single birds were seen to spend long periods in the canopy of local areas on successive days. The possibility that Brown-headed Cowbirds respond to the density of all other species or those that can be parasitized in a forest (Fig. 53) suggests yet another behavioral response contributing to the organization of bird communities.

Male Ruffed Grouse seem to select drumming sites where shrub cover is relatively dense (Gullion, King, and Marshall 1962), especially above two feet (Palmer 1963). They were most abundant in stands with high shrub cover (Fig. 54). Nesting females have been shown to prefer areas offering good visibility in all directions (Gullion 1967). The census method was designed around song birds and was especially poorly suited for nesting females. The data appear to be inconclusive.

DIVERSITY PATTERNS

Various diversity indices for numerical comparisons of the species composition or structural complexity of communities have been used in recent years. According to the accepted concept of diversity, the number of species alone is not an adequate measure. A community having a large number of species with its individuals evenly distributed among them is more diverse than one in which the individuals are distributed among classes unequally. Diversity is related to the degree of uncertainty that a randomly chosen individual will fall into a particular class (MacArthur 1965). However, Tramer (1968, 1969), found that for bird communities there was high correlation between the number of species and the diversity (H') that takes into account both components. He showed that the relative abundance component of numerous bird communities was comparatively constant.

The Shannon-Weiner information function suggested by MacArthur (1965) as a diversity index,

$$H' = -\sum_{i=1}^{s} p_i \log_2 p_i$$

where s = total number of species and p = observed proportion of individuals that belong to the i th species, is influenced by both the number of species present and how evenly or unevenly the individuals are distributed. It was used for all calculations of diversity.

Exactly what diversity indices measure and what their biological significance might be has not always been made clear. The assemblages of organisms studied, commonly called communities, must ultimately be analyzed in terms of energy flow and the arrangement of the organic matter in the habitat in relation to all other habitats and their communities of organisms within the ecosystem. Communities are commonly defined as assemblages of organisms in one taxonomic group using the same habitat. Ecosystems are usually defined in terms of physical and organic components. Within a community, the number and importance of each of the species is commonly called the diversity, but the interconnections between all species on a trophic level are not accounted for. Diversity, therefore, does not completely measure complexity in a community. In addition, the diversity patterns we find in nature may be partly an artifact of the arbitrary nature of the units we measure and how we measure them (Hairston 1969; Barash 1973). However, the use of several different measures of diversity may be a good way to compare habitats to determine if they support comparable assemblages of organisms.

The question of whether a particular habitat is saturated with species, that is, whether it contains the maximum number it may support in terms of structure and energy flow, has intrigued evolutionary biologists, but ecological and evolutionary saturation remains to be demonstrated in complex communities. Until the question of saturation is elucidated, the nature of community structure and function cannot be fully appreciated, and the operational environment of an organism cannot be understood. Elton (1950, 1959, 1966), Patrick (1961, 1963), Cody (1966), and Recher (1969) present evidence of habitats being saturated, while Whittaker (1965), Pianka (1966), and Pielou (1966) review hypotheses explaining the observed differences in diversity in communities that are assumed to be saturated.

TABLE 4
RELATIVE ABUNDANCE AND BIRD SPECIES DIVERSITY IN STANDS WITH LESS THAN 600 TREES PER ACRE

Western Mountains

Summation Data			
Number of Species	Number of Individuals	Diversity Index H′	All Breeding Species Recorded
19	174*	4.3	21
17	102	4.2	20
17	108	3.6	19
16	102	3.6	19
16	96	3.6	19
16	106	3.8	18
16	104	3.8	19
16	58	3.7	18
15	84	3.6	18
15	88	3.4	17
14	80	3.7	18
14	78	3.5	16
14	78	3.8	18
14	76	3.5	16
14	66	3.6	15
13	62	3.4	15
12	58	3.4	15
12	58	3.3	15
11	72	3.2	13
11	48	2.8	13
10	62	3.1	12
9	46	2.9	11
9	56	3.0	11

Parkland

Summation Data			
Number of Species	Number of Individuals	Diversity Index H′	All Breeding Species Recorded
22	122	3.9	26
19	110	3.7	24
17	74	3.8	23
16	134	3.6	19
16	84	3.1	20
15	76	3.4	20
15	76	3.3	21
14	126	3.3	19
14	80	3.0	16
14	118	3.1	19

* Stand 16 had 31 pairs of swallows and numerous other hole nesting birds. Like the stand below it, it was composed of giant very old trees. No stands in the parkland had such large old trees.

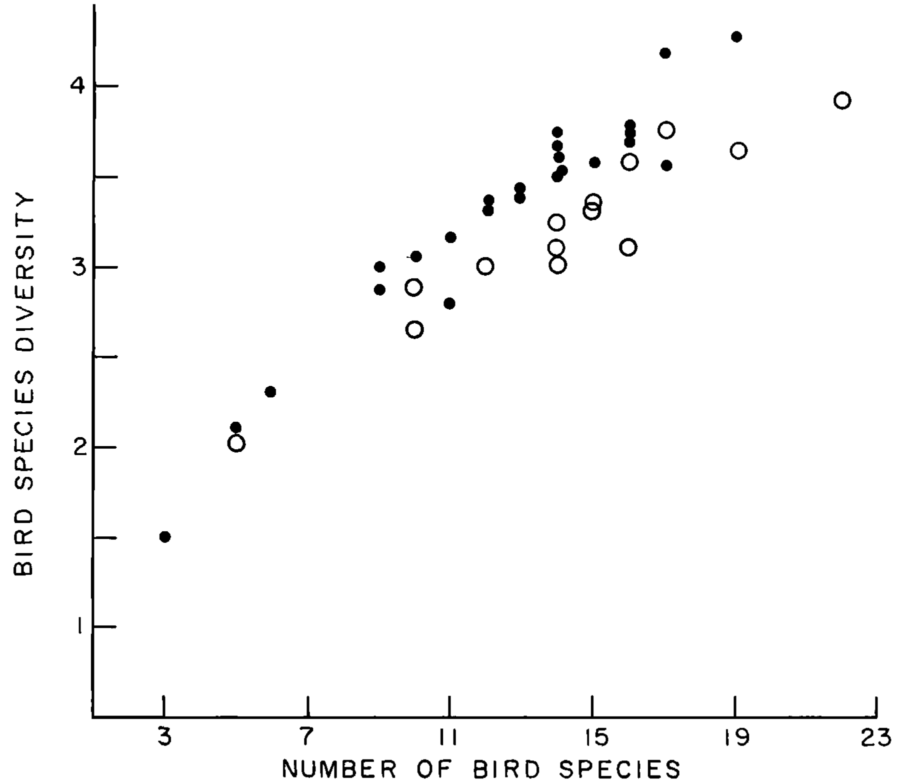


FIGURE 55. Bird species diversity in relation to total bird species in parkland and mountain aspen stands.

The data in Figures 1, 2 and 7 indicate that species diversities based on species summations as measured by one index are very similar in equivalent parkland and western mountain aspen forests, although the maximum number of species and the typical number of individuals is greater in the parkland stands than in the western mountains (Table 4). Unfortunately, I could find few stands composed of large, old trees in Canada for comparison with the numerous old forests in the mountains.

Examination of Table 1 shows that the number of individuals per species in the parkland was less equitably distributed than in the mountains (that is, H′ is less for the same number of species). Figure 55 shows more clearly that for any given number of species, diversity was lower in the parkland than in the mountains. This also shows that the number of species in a stand correlated very well with the diversity index, a relationship found by Tramer (1969) among many bird communities, although not among the lacustrine phytoplank-

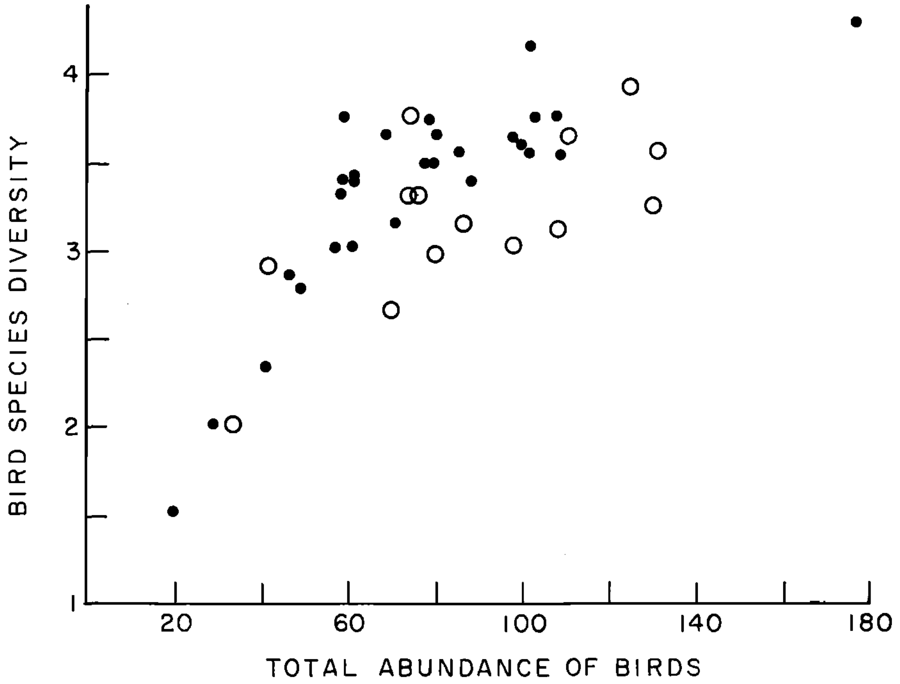


FIGURE 56. Bird species diversity in relation to total abundance of birds in parkland and mountain aspen stands.

ton communities studied by Sager and Hasler (1969). Relative abundance shows a poorer correlation with diversity, especially in the parkland (Fig. 56). The difference shown between the parkland and the mountains, small though it was, strongly suggests that the number of species correlated well only on a local or regional level. This figure is somewhat biased since a greater number of species occurred in the parkland than in the western mountains that could not be included in the summations that were used to calculate diversity. The most diverse parkland stands held more species and individuals than structurally similar mountain stands (Table 4). However, the relative position of the points in Figure 55 does not change.

The greater historical instability of the parkland, previously discussed, may have been responsible for the uncommonness of several widely distributed species. Least Flycatcher populations may be subject to crashes in dry years (Walkinshaw, 1966), and also subject to eventual reduction through competition as the above uncommon species such as Western Wood Pewees, American Redstarts, Great Crested Flycatchers, Tree Swallows, and Mountain Bluebirds become more numerous during a long period of habitat stability. Two

TABLE 5
GEOGRAPHICAL REPLACEMENT OF MORPHOLOGICALLY SIMILAR SPECIES*

Western Mountains			Parkland			
Arizona	Central Mts.	Wyoming	Foothills	Sask.	Manitoba	Boreal
Canopy						
			Eastern Kingbird ———	———	———→	
			Least Flycatcher ———	———	———	———→
			Red-eyed Vireo ———	———	———	———→
Warbling Vireo ———	———	———	- - -	- - -	- - -	- - →
Audubon's Warbler ———	———	———→				
			Baltimore Oriole ———	———	———	———→
Western Tanager ———	———	———	———→			
Evening Grosbeak (Arizona only)						
				Purple Finch ———	———	———→
	Cassin's Finch ———	———→				
Shrubs						
			Black-billed Cuckoo ———	———	———→	
Empidonax flycatcher ———	———	———	———→			
			Gray Catbird ———	———	———→	
		Yellow Warbler ———	———	———	———	———→
				American Redstart ———	———	———→
			Rose-breasted Grosbeak			
Black-headed Grosbeak ———	———	———	———→			
Green-tailed Towhee						
			Rufous-sided Towhee			
Chipping Sparrow ———	———	———	- - -	- - -	- - -	- - →
			Clay-colored Sparrow ———	———	———	———→
Holes						
			Yellow-shafted Flicker ———	———	———	———→
Red-shafted Flicker ———	———	———	———→			
			Pileated Woodpecker ———	———	———	———→
Violet-green Swallow ———	—→					
	Tree Swallow ———	- - -	- - -	- - -	- - -	- - →
	Black-capped Chickadee ———	———	———	———	———	———→
White-breasted Nuthatch (Arizona only)						
			Red-breasted Nuthatch ———	———	———	———→
Pigmy Nuthatch (Arizona only)						
Western Bluebird (Arizona only)						
Mountain Bluebird ———	———	———	- - -	- - -	- - →	
Ground						
		Ruffed Grouse ———	———	———	———	———→
Hermit Thrush ———	———	———	———	———	———	———→
			Veery ———	———	———	———→
				Ovenbird ———	———	———→
			Connecticut Warbler ———	———	———	———→
				Mourning Warbler ———	———	———→
	MacGillivray's Warbler ———	———	———→			
		Pink-sided Junco (Wyoming)				
Gray-headed Junco ———	—→					
	White-crowned Sparrow ———	———	———→			
			White-throated Sparrow ———	———	———	———→

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* The ranges of species within aspen forests are indicated by the arrows. Dashed lines indicate lower relative abundance. Similarity in body size, and beak size and shape were the basis for the comparisons. Species are grouped according to nesting guilds.

species in the parkland, the Baltimore Oriole and Ovenbird, show great reductions in abundance at the edge of their ranges, introducing furter unevenness in relative abundance.

What is the evidence that these habitats are saturated? Within both major regions the total number of species found breeding in all forests is roughly twice the number found breeding in any one mature stand, suggesting an equilibrium number. Also, over very large geographical areas, the total number of species in like stands within each region is similar, in spite of compositional differences. In the foothills area (28–30), where the total number of species potentially breeding in aspen is largest, numbers per stand are typical of parkland. The presence of two common species in the parkland (Cedar Waxwing and Common Goldfinch), which breed late in the season, suggests temporal adaptation to a rich community. Diversity is correlated with forest structure within each region. That is, a stand achieves maximum diversity during the life cycle of the forest. Finally, there are a number of geographical replacements by species that would be expected to compete if sympatric, because of their similar morphology and behavior (Table 5).

Evidence against saturation is also circumstantial. Number of breeding species in parkland stands is higher than in the western mountains, and there is strong evidence that historical factors have both decimated elements or prevented their establishment in the parkland, and that with their establishment, diversity (H′) will increase somewhat. It is possible, of course, that as these elements increase, interactions will result in decreases of other species. However, stands in the western mountains having high populations of cavity nesting birds, including some of those potentially able to increase in the parkland, do not show corresponding decreases in other species. In addition, the inequality of species abundance and of guild diversity (Fig. 7 and Fig. 55) in the parkland may be a temporary feature of disturbance and if it adjusts towards greater equitability, diversity will increase. Tramer (1968) similarly concludes that "disturbance of the native vegetation would probably produce wide amplitude oscillations in bird species abundance, which in turn could possibly (but not necessarily) lower values of equitability and evenness." The already higher number of species in the parkland and the potential for diversity (H′) to increase may be attributable to the favored geographic position of the parkland in which montane, boreal, and eastern species contribute to a larger pool of appropriate species (see Udvardy 1963).

New species can successfully invade a community without eliminating other species by further division of resources already in use, or by exploitation of unused resources, the latter process being untenable to many ecologists who believe that most communities are closed or saturated. There is evidence that some species adjust their patterns of habitat exploitation under the first set of conditions (Lack 1942; Crowell 1961, 1962; Sturman 1968a), although not always (Orians, 1969a), but the success of the latter group would not be affected by species already in the community. The latter class of organisms might be called appropriate for that habitat because it is capable of invading it without replacing other species. The close correlation between abundance and forest structure for some species strongly suggests that many such species are adapted to a portion of the habitat and are more or less independent of other factors, such as the presence of other species. Although several morphological replacements are conspicuous, there appear to be a greater number of species in the western mountains that are not replaced (Table 5). Appropriate species may be absent from the region.

Equally significant may be the increased number of morphological types found in a given strata in the parkland (Table 5). When considering, for example, the number of species and individuals nesting in the canopy including species not in the summation, numbers were highest in the foothill stands and the most mature (32, 35, 39) forests of the parkland (Table 1). The absence of six shrub and ground nesting species in stand 30 as a result of its geographic position is discussed under faunal affinities.

For the above assertions to be meaningful, it must be shown that the more rigorous climate of the mountains is not responsible for lowered diversity. That climate is possibly not limiting may be evident from stands 28–30 that had some of these montane climatic features, but that also had many parkland avifaunal affinities and high numbers of species and individuals per stand.

Finally, the diversity of stand 34, in the boreal region, falls below other stands, although the boreal forest is continuous with the parkland. This stand was clearly not saturated on the basis of its structural potentialities, although it may prove to have been saturated with reference to its features such as productivity. Climatically, the boreal region suffers fewer extremes than the parkland (Currie 1953). This means that the shorter growing season and cooler temperatures are the only factors that could be rigorous. This may result in later and lower production of some kinds of insects, particularly large arboreal types. Foliage gleaning species were less abundant in stand 34. In the Yukon, foliage gleaning and flycatching birds are further reduced (Drury 1953). On the other hand, pure aspen forests covering millions of acres in lieu of coniferous forests may be a relatively recent boreal phenomenon, associated with warmer and drier post-Pleistocene climates. Wells (1970) presents evidence that this has occurred in the last 900 years following regional fires. Therefore, we might speculate that the majority of boreal birds have adapted themselves to two important features of the environment: coniferous physiognomy and two or more weeks of frosts during the first part of the breeding season. With the appearance of enormous tracts of a habitat structurally identical to the parkland but with a boreal climate, and only two sources of species, one with an entirely different physiognomy and one with a warmer climate, neither ecological or evolutionary saturation should be expected. Stands 1–4 in Arizona may illustrate the importance of a diversity of surrounding habitats in contributing species to a community isolated from other sources. Ten species common to more northerly montane aspen forests were completely missing in the Arizona stands, but diversity has not decreased, due partly to the invasion of these stands by species from the surrounding habitats. Similarly, aspen forests in Minnesota (Hickey 1956) and Wisconsin (Beals 1960) differ somewhat in species composition from the parkland, but are highly diverse. There is a great variety of habitats in these areas from which species may be derived. Terborgh and Weske (1969) speculate that the lower numbers of bird species in some secondary tropical habitats is the result of isolation from the rich sources of species in primary vegetation, and Orians (1969) suggests historical isolation resulted in low numbers of bird species in one Costa Rican forest. Tramer (1968) describes a situation in Georgia somewhat the reverse of that in stand 34. The low diversity of pine plantation bird populations may be the result of isolation from other coniferous forests. In spite of habitat adaptations on small British Islands, Lack (1942) concludes that saturation is not achieved.

Ecologists are looking for some universal principles that govern populations in communities, and they have assumed ecological saturation of most habitats as a necessary prerequisite (Pianka 1966), in spite of the scanty nature of the evidence. Local geography and history have been assumed to have minor or no influence (Recher 1969). Ecologists have implicitly and uncritically accepted the notion that nature abhors a vacuum. The evidence here is that to properly fill such vacuums, time in both the ecological and evolutionary senses is required. Both geographical isolation as in the western mountains, instability as in the parkland, and low regional habitat diversity combined with isolation as in the boreal region, may result in communities in which species composition equilibrates, or reaches a local maximum level, below the maximum possible for the habitat. In addition, it is assumed by many (e.g. Pianka 1966) that the number of habitats in a region and the bird species diversity of a single habitat are unrelated, an assumption not supported by data from stand 34 and stands 1–4. The artificial nature of the habitat categories by which we define our community of bird populations seriously limits the meaning of saturation, as discussed below.

The data presented only suggest that some aspen forests are not saturated with bird species on the basis of the structure of these forests. Since other features of these forests such as climate are not uniform it cannot be said with total confidence that a lower diversity is not the maximum for a region. Yet because the resulting community lacks species appropriately suited to the peculiarities of the habitat, it does not seem reasonable to assume that the community will maximize resource use simply by the combined plasticity of response

TABLE 6
UNCOMMON BIRDS (F < 35%) ARRANGED BY THE
STRATA IN WHICH THEY NEST

Western Mountains	
Birds	Habitat in which more common
Canopy	
Red-tailed Hawk	Open areas with patches of forest
Great Horned Owl	Open or patchy deciduous forest
Long-eared Owl	Patchy deciduous forest
Western Tanager	Conifer forest
Evening Grosbeak	Spruce forest
Shrubs	
Mourning Dove	Numerous open habitats
MacGillivray's Warbler	Riparian forest and brush
Lazuli Bunting	Shrubby uplands
Green-tailed Towhee	Shrubby uplands
Lincoln's Sparrow	Wet places, bogs
Song Sparrow	Wet shrubby areas
Holes	
Hairy Woodpecker	Mature forest
Purple Martin	Towns, farms
White-breasted Nuthatch	Mixed and some conifer forests
Pigmy Nuthatch	Pine forest
Western Bluebird	Lower elevations than Mountain Bluebird
Ground	
Townsend's Solitaire	Forest near ledges, canyons

Parkland	
Birds	Habitat in which more common
Canopy	
Broad-Winged Hawk	Extensive forest
Black-billed Cuckoo	Riparian forest
Eastern Kingbird	Edges
Purple Finch	Conifer and mixed forest
Shrubs	
Dusky Flycatcher	Open conifer
Gray Catbird	Shrubby edges
American Redstart	Shrubby deciduous forest
Rufous-sided Towhee	Riparian thickets
Holes	
American Kestrel	Various open
Yellow-shafted Flicker	Various open forest
Pileated Woodpecker	Mature deciduous forest
Great Crested Flycatcher	Mature deciduous forest
Red-breasted Nuthatch	Mixed forest
Ground	
Connecticut Warbler	Some bog types; nowhere common
Mourning Warbler	Aspen forest in midwest

of the species present. Orians (1969a) has noted such an apparent lack of response in an isolated rain forest. If the assumption that most continental habitats are saturated with organisms has important exceptions, the recognition of their influence on community stability (Loucks 1970) and possible role in processes of speciation (i.e. habitat adaptations, Lack 1942) should be considered.

Concentration of dominance is most often described for a single taxonomic group occupying a habitat that is arbitrarily defined by a dominant characteristic of the vegetation, soil, or water. The continuous or dependent nature of such assemblages is temporarily or completely ignored. As a result the species populations of the designated habitat are not considered in light of other habitats in which the species occur. Since a species is characterized by its entire gene pool, the environment of the population in the habitat studied represents only a part of the environment of the whole species. The success of each of the members of a particular community studied is, therefore, the product of factors both within that habitat and within other habitats. Concentration of dominance in a given community may not be solely a function of the structure, productivity, stability or age of that habitat, but also may be influenced by surrounding habitats in which the species also occur.

Thirty-four species recorded as breeding in the stands are uncommon or rare (frequency $< 35\%$) in aspen forests (Table 6). One of the smaller species, the Connecticut Warbler, does not appear to be abundant in any other habitats, and five of the larger species, hawks, owls and corvids, are never abundant in other habitats. It should be expected that energy requirements of larger (heavier) species necessitate larger territories and are responsible in part for lowered abundance (Schoener 1968), leaving the one small species that is genuinely rare in all habitats, and for which I have no explanation. Are such populations most liable to extinction and are they on their way out? Were they once abundant in some now uncommon habitat? Do they have highly specialized requirements that have not been detected?

Of the 34 common species (Table 7) in aspen forests, 19 are found in both regions although several are less abundant in one or the other, or do not range completely through a region. All 34 species may be considered uncommon in certain other habitats in which they breed (Table 7; see Bond 1957 and Beals 1960 for graphic demonstrations over a continuum of habitats). Concentration of dominance is, therefore, partly a function of measuring relative abundances in restricted habitats or over restricted areas.

The fact that the abundance of several species is related to features of the vegetation suggests that these features are of primary importance to regulation of abundance. Competition or avoidance of competition influences such relationships in both historical and immediate ways (Sturman 1968a, b; Lack 1969). Specialization or restriction in a community, then may be as much a

TABLE 7
COMMON (F > 35%) BIRDS ARRANGED BY THE STRATA IN WHICH THEY NEST

Birds	Western Mountains	Foothills Parkland	Parkland
Canopy			
Western Wood Pewee	1	2	2
American Robin	1	2	2
Cedar Waxwing	P	1	1
Red-eyed Vireo	*	1	1
Warbling Vireo	1	2	2
Audubon's Warbler	1	*	*
Baltimore Oriole	*	2	1
Cassin's Finch	1	*	*
Pine Siskin	1	1	*
American Goldfinch	4	1	1
Shrubs			
Broad-tailed Hummingbird	1	*	*
Empidonax flycatcher (Sp?)	2	3,4	*
Least Flycatcher	*	1	1
Yellow Warbler	2,3	1	1
Pheucticus Grosbeak	2	1	1
Chipping Sparrow	1	4	4
Clay-colored Sparrow	*	1	1
Holes			
Common Flicker	1	4	4
sapsuckers	4	1	1
Downy Woodpecker	4	1	1
Violet-green Swallow	3	*	*
Tree Swallow	1	4	4
Black-capped Chickadee	3	1	1
House Wren	2	1	1
Mountain Bluebird	1	4	4
Ground			
Ruffed Grouse	3,4	1	1
Hermit Thrush	3	2	2
Veery	*	1	1
Ovenbird	*	*	1
+ Brown-headed Cowbird	4	1	1
Junco Species	1	*	*
White-throated Sparrow	*	1	1

1. Bird relatively very common to abundant. 2. Common, but less so than in other region(s). 3. Scarce or absent in part of the region. 4. Present in the region but uncommon (f < 35%). * Absent. + Brood parasite. Where a morphological equivalent is completely missing, examination of Table 6 provides insight into uncommon species that might partly fill vacancy.

result of historical factors as of immediate factors. In addition, some uncommon species of irregular occurrence may be the surplus from the more suitable habitats or from a good year (Orians 1969b; Weaver and West 1943). Therefore, the phenomenon of concentration of dominance may be a product of

TABLE 8
REGIONAL AFFINITIES AND FREQUENCY OF OCCURENCE (F)
OF THE BREEDING BIRDS OF ASPEN FORESTS

Exclusively Montane*	M/f	P/f	Both Regions	M/f	P/f
A.			C.		
Red-shafted Flicker*	67	14	Red-tailed Hawk	P	P
Empidonax flycatcher*	82	7	American Kestrel	P	P
Purple Martin	4		Ruffed Grouse	15	100
White-breasted Nuthatch	4		Great Horned Owl	4	7
Mountain Bluebird*	74	P	Long-eared Owl	4	7
MacGillivray's Warbler*	11		Yellow-bellied Sapsucker	26	57
Black-headed Grosbeak*	40	7	Hairy Woodpecker	22	21
			Downy Woodpecker	30	50
B.			Western Wood Pewee	89	43
			Tree Swallow	37	14
Broad-tailed Hummingbird	67		Black-capped Chickadee	44	71
Violet-green Swallow	30		House Wren	82	93
Pigmy Nuthatch	4		American Robin	85	64
Western Bluebird	11		Mountain Bluebird	74	P
Townsend's Solitaire	7		Warbling Vireo	100	86
Audubon's Warbler*[1]	85		Yellow Warbler	30	71
Western Tanager*	7	7	Brown-headed Cowbird	26	100
Evening Grosbeak	11		American Goldfinch	4	71
Cassin's Finch*	40		Chipping Sparrow	40	21
Pine Siskin*	77	29	Song Sparrow	15	21
Pink-sided Junco* Gray-headed Junco	100		D.		
White-crowned Sparrow*	26	14	Hermit Thrush	59	36
			E.		
			Mourning Dove	P	P
			Common Raven	P	P
			Starling	4	P

Exclusively Parkland	P/f
F.	
Broad-winged Hawk^{+}	7
Black-billed Cuckoo	14
Ruby-throated Hummingbird	21
Yellow-shafted Flicker^{+}	14
Pileated Woodpecker	14°
Eastern Kingbird	21
Great Crested Flycatcher	21
Least Flycatcher	100
Common Crow	P
Gray Catbird	29
Veery	50
Cedar Waxwing	86
Red-eyed Vireo	86
Ovenbird^{+}	36
Connecticut Warbler^{+}	P

TABLE 8 (continued)

Exclusively Parkland	P/f
Mourning Warbler[+]	14
American Redstart	21
Baltimore Oriole[+]	79
Rose-breasted Grosbeak[+]	57
Rufous-sided Towhee	14
Clay-colored Sparrow	43
White-throated Sparrow[+]	57
G.	
Red-breasted Nuthatch	29
Purple Finch	7

A. Having a population or closely related species in eastern deciduous habitats. B. Having a population or closely related species restricted to the west or to coniferous forest. C. Having a population or closely related species in deciduous habitats. D. Having a population in coniferous forest. E. Having a population typically in habitats other than aspen forest. F. Having a population or closely related species in eastern deciduous habitats. G. Having a population in coniferous forests. M/f = frequency in stands 1–27. P/f = frequency in stands 28–41. [*] These eleven species are also found in the foothills or Cypress Hills but are considered to be montane. [+] The ranges of these species (except the Great Crested Flycatcher) end in or near the north end of the foothills where the parkland occurs at lower elevations than to the south. [°] This species was recorded much less frequently than it actually occurred (43%). [1] Myrtle Warblers appear to breed in some poplar forests (see Drury, 1953).

methods of measurement, historical factors, occurrences in other habitats, and species interactions in a local area.

AVIFAUNAL AFFINITIES

The geographic origin of local faunas may be approached from a static regional standpoint or from a dynamic standpoint concerned with the mixing and interdigitation of separate faunas (Voous 1963). Udvardy (1963) points out that "the present distribution of species, in relation to the distribution of communities, is the clue to understanding the zoogeographical picture of the past, including the evolution of the species and the dynamics of their range." In particular, the breeding range is important.

There are 24 species in both montane and parkland aspen forests, including a large percentage that are of frequent occurrence. Twenty species are exclusive to montane and 24 exclusive to parkland stands. If these groups are further divided according to the habitats in which populations of each species or its closest eastern relative (such as Yellow-shafted and Red-shafted Flickers) are most abundant, then montane aspen forests have a greater number of species than the parkland, which are probably derived from either coniferous forests or other habitats (Tables 8 and 9; see also the species accounts). Closer examination shows that seven out of 25 important species (frequency of occurrence $< 25\%$) in montane aspen forests are either completely western in distribution (with no eastern close relative) or are more commonly found in coniferous forests or other habitats. Yet, only one species from the group

TABLE 9
SUMMARY OF REGIONAL AFFINITIES AND SOURCES OF SPECIES

Montane Aspen Forests			Parkland Aspen Forests
	Major Populations (frequency > 25%)		
No. of Species			No. of Species
Montane Region only			Parkland Region only
From coniferous forests	4	1	
From deciduous habitats	5	12	
Other	3	0	
Common to both regions			Common to both regions
From coniferous forests	1	1	
From deciduous habitats	12	11*	
	Minor Populations (frequency < 25%)		
Montane Region only			Parkland Region only
From coniferous forests	5	1	
From deciduous habitats	3	9	
Other	0	0	
Common to both regions			Common to both regions
From coniferous forests	0	0	
From deciduous habitats	8	9*	
Other	3	3	
Totals			
Conifer	10	3	
Deciduous	28	41	
Other	6	3	

* Discrepancies are the result of excluding a species of < 25%f.

common to both regions is more common in coniferous forests, and one important species from the parkland is more abundant in coniferous forests. Of the minor species (f < 25%), those presumed to be derived from deciduous habitats also predominate in all groups, although coniferous forest birds or birds from other habitats are more evident in the montane region. Within each region most of the important and many of the minor species occur in aspen forests throughout each geographic area. Montane aspen forests are presently isolated from the parkland by the scarcity of small clones and the absence of aspen forests in the extensive region between southern Montana and the parkland in northern Montana.

Why are there strong resemblances to, and affinities with, eastern deciduous forests? What is the explanation for the greater influence of western and coniferous forest species in montane aspen forests, and why are there more local differences in the montane avifauna than in the parkland (Table 10)?

TABLE 10
AFFINITIES WITHIN REGIONS

Western Mountains						
Throughout	S.	S-cent.	Cent.	Cent-n.	N.	Special*
Red-shafted Flicker	White-breasted Nuthatch	Broad-tailed Hummingbird	Purple Martin	Tree Swallow	Ruffed Grouse	Mallard
Empidonax flycatcher	Pigmy Nuthatch	Violet-green Swallow	Starling	Black-capped Chickadee	American Goldfinch	Townsend's Solitaire
Audubon's Warbler	Western Bluebird	Hermit Thrush		Yellow Warbler	Pink-sided Junco	Lazuli Bunting
Black-headed Grosbeak	Evening Grosbeak	Gray-headed Junco		MacGillivray's Warbler		Green-tailed Towhee
Pine Siskin				Cassin's Finch		Lincoln's Sparrow
				White-crowned Sparrow		

Parkland			
Throughout	Foothills	Rest of Parkland	Special*
Black-billed Cuckoo	Red-shafted Flicker	Broad-winged Hawk	Lesser Yellowlegs
Ruby-throated Hummingbird	Dusky Flycatcher	Yellow-shafted Flicker	Common Grackle
Pileated Woodpecker	Western Tanager	Great-crested Flycatcher	Lazuli Bunting
Eastern Kingbird	Black-headed Grosbeak	Ovenbird	
Least Flycatcher	Pine Siskin	Connecticut Warbler	
Red-breasted Nuthatch	White-crowned Sparrow	Mourning Warbler	
Gray Catbird		American Redstart	
Veery		Baltimore Oriole[+]	
Cedar Waxwing		Rose-breasted Grosbeak	
Red-eyed Vireo		White-throated Sparrow	
Rufous-sided Towhee		Purple Finch	
Clay-colored Sparrow			

Abbreviations: S. = South, S-cent. = South-central, Cent. = Central, N. = North. *Unusual conditions adjacent to forest studied, such as rock outcropping or lake. [+] The Baltimore Oriole has extended its range into the northern part of the foothills, but it occurs in the river bottoms (lower elevations) farther south.

Concerning avifaunal affinities, the importance of deciduous forest species in aspen forests of the western mountains, rather than birds from coniferous and other surrounding habitats, suggests that the present isolation of these forests from the east, or some other source of species, has been broken down in the past. Moreover, it may demonstrate the importance of specific adaptations to deciduous forests resulting from long association with either Arcto-Tertiary or eastern deciduous forests (See Appendix 2). Beginning with the development of montane upland poplar forests during mid-Cenozoic times (discussed below), and ending with their most recent isolation in late Pleistocene or recent times, the surrounding coniferous forests and other habitats would presumably have been a ready source of bird species competing for a place in the new habitat. The great mobility of aspen seeds has probably contributed to the establishment of aspen forests in isolated areas, such as in central Arizona. The uniformity of bird species composition within regions, despite these disjunctions must be a function of more than the ability to disperse rapidly, because upon arrival in a new aspen forest, a bird presumably would have to contend with local but possibly less well-adapted species invading from surrounding habitats. At the same time, the fact that widely separated forests differ somewhat in composition (Table 10) demonstrates the operation of local modifying influences.

During the Miocene and possibly extending into the mid-Pliocene, Arcto-Tertiary deciduous forests characterized much of mid-continental North America (Axelrod 1948; Chaney 1947, 1959). The progressive loss of broadleaf trees was occurring during this time (MacGinitie 1953, 1958), but oaks, maples, beech and poplars, including possibly two aspens, were present on the Columbia Plateau during the Miocene (Chaney 1959). The leaves of *Populus voyana* in this flora are similar to those of *Populus tremuloides* (Chaney and Axelrod 1959). The ancestry and origin of the present *P. tremuloides* in the west is not yet understood (Barnes 1967), but it is reasonable to assume that at least one upland poplar remained in the mountains while other deciduous trees were lost as a result of topographic and climatic changes (Dix 1964). An hypothesis of Barnes (1967) to explain unusual leaf morphology in some aspen clones from Idaho implies the persistance of aspen in the mountains since the Miocene. By the late Pliocene, western poplar and coniferous forests were separated from eastern deciduous forests by the Great Plains (Dix 1964; Hubbard 1969) where the only wooded areas occurred along watercourses (Chaney and Elias 1936).

Reconstruction of the role of aspen and other poplars in western and northern forests during the Pleistocene is difficult because aspen pollen is poorly preserved at best, and macrofossils are not common as would be hoped and frequently cannot be identified. Nevertheless it is reasonable to assume that the general patterns of movement of the constituents of the Cordilleran and boreal coniferous forests during this time were also those followed by aspen. The events important to bird populations during this time were summarized, mapped, and discussed by Rand (1948) and Mengel (1964), and certain important details were updated by Hubbard (1969). Short (1965) provides an excellent and comprehensive review of events beginning in the Pliocene. In summary, during drier interglacials Cordilleran forests showed internal disjunctions but were continuous with boreal forests at higher latitudes in the northwest. Vegetation was probably similar to that of recent times (Love 1959). During glaciations boreal forest might have existed over large parts of the Great Plains of the United States (Wells 1970), but it is not clear that the boreal forest simply moved south or north in front of the advancing ice or that it was always continuous (Love 1959). Forests also persisted in the Yukon Valley. Cordilleran forests moved down, and those on the front range moved somewhat east as a result of the more mesic conditions in the high plains and foothills. It is probable that elements of the two met and mixed at different times in this area, but there was a disjunction between the forests of the western high plains and the interior Cordilleran forests caused by ice and tundra at higher elevations to the west (Hubbard 1969). Post-Wisconsin aridity resulted in die-off and re-establishment of forests at higher elevations and farther north, resulting in the present groves and forests of aspen that are generally of vegetative origin and may be regarded as the remains of more extensive or continuous post glacial forest in the parkland (Maini 1960) and mountains. Recent evidence (Wells 1970) suggests that die-off and retreat of forests was more recent in some areas than was previously suspected.

Mengel (1964) and Hubbard (1969) seem to have assumed that these forests were coniferous, but it is highly probable that aspen was a major constituent in both regions during drier periods (as now), with possibly fewer pure stands during wetter periods because of the reduced frequency or importance of fire. The present aspen forests surveyed in this study (*P. tremuloides* var. *aurea*) are probably derived from populations that survived in the mountains south of or below the ice and in the Yukon Valley, and therefore invaded from several directions (Maini 1960).

It is conceivable that whenever there was boreal forest, a parkland-like habitat existed on its southern boundary, and that during glaciations it ended in the foothills or high prairies farther south, much as it does in Alberta today. There is some evidence that parkland existed in the Prairie Provinces during the Late Pleistocene (Love 1959; Ritchie and de Vries 1964). The very small relict clones of aspen found between the southern extent of the parkland and the nearest aspen forest in southern Montana may represent a recent or possibly Pleistocene parkland. Die-off in this area may have occurred in the last 900 years (Wells 1970). If this were the case, then parkland and Cordilleran forests and bird populations may have mixed at various times at lower latitudes on the eastern side of the mountains much as they do today (Hansen 1949), but there would always have been a disjunction due to topography between these communities and those of the interior farther west.

If monotypic or aspen-conifer forests had their origin in the mountains during the Pliocene, then certain bird species or ancestral populations adapted to decidous forests were derived directly from the Arcto-Tertiary forests and then isolated to some unknown degree in the west. Since that time events of the Pleistocene and recent times have greatly complicated the original pattern.

As a result, dispersal west via parkland-like corridors may have been feasible, with bird populations being separated in interior Cordilleran, eastern forest or boreal-parkland, and Yukon Valley regions during glaciations. Poplars and other deciduous species in the valleys of the rivers such as the Missouri and Platte may also have provided corridors to the west during certain periods (Short 1965). The latter unglaciated region may have been more heavily forested than Hubbard supposes, including aspen forest. One other point of contact between Cordilleran and deciduous forest, especially oak, may have existed in the Texas-New Mexico area (Hubbard 1969; Wells 1970). However, the more southern aspen forests especially in Arizona show more influence of bird populations from surrounding habitats than more northerly forests (Table 10).

During glaciation a bird population in the far western parkland may have adapted itself somewhat to the hybrid biotic and climatic conditions of the foothills. Increasing post-glacial aridity would have resulted in a retreat of aspen both altitudinally and latitudinally causing these forests and their bird populations to become disjunct, as they are now. If suitably adapted, a population derived from an eastern species could adjust to the montane conditions and finally invade interior Cordilleran aspen forests during an interglacial. A subsequent glaciation would complete its isolation from parkland and more eastern populations. Similar processes could have occurred in Alaska.

Since it is unlikely that more than a few species from the parkland would be suitably fit to survive the post-glacial retreat into the mountains, the process of exchange should be slow. This process has probably prevented extensive recent colonization of the mountains from the east such as has occurred in the parkland. The faunal groupings of Udvardy (1963) indicate at least four sources of bird species for the parkland, but the parkland avifauna is largely a depauperate extension of eastern deciduous forest with two western species, the Mountain Bluebird and Western Wood Pewee. The process may be a cause of the major compositional differences found between the two regions. The greater number of western and coniferous forest birds successfully established in montane aspen forests in contrast to parkland forests may have part of its cause in barriers to westward dispersal of deciduous forest bird species. If parkland and interior Cordilleran aspen forests had been continuous during glaciation, one would expect a larger exchange to have taken place.

Bird species characteristic of the parkland and also found in the foothills (Table 8) might represent a group that is becoming adapted to hybrid biotic and climatic conditions of the foothills and from which a population could become adapted to montane conditions. Some of these species are found in other habitats in the region south of the parkland. Those species that drop out before the end of the essentially continuous aspen of the foothills area may represent species with no present potential for invading western aspen forests (Table 8).

The presence in the western aspen forests of numerous species presumably derived from deciduous forests in the Pleistocene is evidence that exchange occurred. Some have almost surely had their origins in the west during the Pliocene, however, and others are clearly derived from other habitats. Western riparian forest bird communities include most of the species found in montane aspen forests (Miller 1951) and have probably been important in the processes described.

The local differences in species composition found in the two regions, in contrast to the major compositional differences between regions, have probably been most shaped by ecological rather than historical factors. For example MacGillivray's Warblers and Yellow Warblers occur in the southern Rocky Mountains, but the aspen forests of that area are xeric and essentially shrubless and are therefore not suitable habitat for those species. Aspen forests in Wyoming appear suitable for Least Flycatchers, but this species does not occur west of the front range.

Compositional differences are greatest between stands most distant from each other; mature stands in Arizona show greater contrasts to those in Manitoba and Saskatchewan than to any others (Table 10). Minor differances are of a continuous nature, but there are four places where the ranges within aspen of numerous bird species end together. The central mountain region (Utah and Colorado) represents the southern limit of six species, five of which are common. Four more species are restricted to the southern stands (Table 10). There is therefore a strong gradient representing a difference of ten species between the south central region and the southern region. A difference of seven species is found between northern stands (Wyoming) and those to the south.

The causes of these differences can only be suggested in a few cases. Further comments are found in the species accounts. All four species found only in the south invaded from other habitats, in the absence of a number of species found in most other regions. The overlap in Utah and Colorado in the habitat occupancy of the Violet-green and Tree Swallows suggests habitat separation between these widely sympatric species. The juncos hybridize and to some degree grade into one another from area to area and behave ecologically as the same species. The ranges in all habitats of the Tree Swallow, Black-capped Chickadee, Cassin's Finch and White-crowned Sparrow all end north of the southern stands (1–7). The ranges of the Ruffed Grouse and American Goldfinch end at or near the northernmost stands in Utah and Colorado. Aspen is a rather minor and quickly replaced component of most forests south of Utah, and this may be related to the distribution of these bird species, but other factors must also have been involved.

It has been stated that there are 24 species found breeding in both regions. In addition, there are 11 species of birds classified as exclusive to montane stands that breed in parkland aspen forests in the foothills or Cypress Hills (immediately east of the foothills, Fig. 1, Table 8). Audubon's and MacGillivray's Warblers, juncos and Cassin's Finch were not recorded breeding in the foothills stands studied, although the first three breed in foothills aspen farther south or in aspen forests in the Cypress Hills (Godfrey 1950; Halladay 1965; Bird and Halladay 1967). Of the 24 species classified as exclusive to the parkland, the southwestern edge of the ranges of ten species end at the transition from prairie parkland to foothills parkland (Table 10).

Since the forests are essentially continuous in this region (The Bow, Highwood and Oldman Rivers divide three blocks of forest and grovelands between Waterton Park in the southwest and the area north of Calgary), the ecology of all these species warrants further investigation. As already discussed, the foothills are climatically intermediate between montane and prairie parkland regions. The presence in the foothills of 11 montane species, of which only 6 occur regularly in foothills aspen, and in the same region, the presence of 12 breeding parkland species and absence of 10 recorded regularly elsewhere in the parklands strongly suggests that the foothills are not only climatically intermediate but biotically intermediate. Climatic influences, competitive exclusion and historical factors should be considered in any explanations of breeding ranges of these species.

The absence of Audubon's and MacGillivray's Warblers, Cassin's Finch and a junco in the foothills is peculiar since they are found breeding to the east in the Cypress Hills. It would be fruitful to investigate competitive factors, since a number of important parkland foothills birds are absent in the Cypress Hills. I do not have an explanation for the fact that the Pine Siskin and Western Tanager do not breed in the parkland, since they do not seem dependent on conifers in the mountains. The Dusky Flycatcher is abundant in Cypress Hills aspen forests where Least Flycatchers are uncommon (Halladay 1965; Bird and Halladay 1967), indicating possible competitive exclusion.

The Black-headed Grosbeak has not extended its range north to meet that of the Rose-breasted Grosbeak, nor have the ranges of the White-crowned and White-throated Sparrows met in this area. The flickers interbreed in this area (Short 1965) and sapsuckers probably also interbreed here.

Wells (1970) presents evidence for a mid-continental trend towards more xeric conditions in the last 900 years and suggests that aspen rapidly replaced spruce and other conifers over a large area at this time. It is possible that prior to this occurrence the narrow band of aspen and poplar forest that connects the more expansive parkland northeast of the foothills with that of the foothills well to the south (Atlas of Alberta 1969) did not exist, or was not so nearly continuous until fire burned the conifers regionally. As a result only a short time has elapsed since aspen forest was present in this region and bird species are still expanding their ranges in both directions. This could also account for the continuing range extensions to the south and into the foothills by the Connecticut Warbler, Ovenbird, and Baltimore Oriole.

This only explains present gaps between species ranges and does not explain satisfactorily why there have been so few successful invasions of the parkland from the west when such a possible habitat disjunction was not present. It has already been pointed out that a large number of the bird species classified as exclusive to the montane stands (Table 8) are clearly invaders from other surrounding habitats, in contrast to the numerous species exclusive to the parkland and poplar woodland that seem to have been derived from deciduous habitats. Species shared by both regions include many that seem well-suited to the habitat. This suggests that the eastern deciduous forests are a rich source of species for new deciduous habitats, while montane habitats have a much poorer group of species suited to deciduous forests. Thus there should be a higher frequency of occurrence of appropriate morphological types from the east suited for exploitation of unused resources in deciduous habitats than from the west.

Short (1965) suggests another explanation. "The eastern affinities of the avifauna of northwestern Canada are attributable to the fact that this area became available to eastern, rather than western, forms; the central Canadian corridor is the probable cause of this phenomenon." Short must have assumed that populations of western forms were not present on the eastern side of the front ranges during the late Pleistocene, or that such populations were not able to advance into the corridor in the same way as eastern forms as forest developed.

The success of a number of eastern species in the foothills and lack of success of others, the absence of several western species in those forests (although present in the area), and the ending of the ranges of numerous western species and forms in the climatically intermediate transition zone from foothills to plains parkland, including Red-shafted Flicker, is evidence that ecological factors rather than purely historical events, have been important in the development of an essentially eastern avifauna in northwestern Canada.

SPECIES ACCOUNTS

The following discussion of the bird species recorded in aspen forests follows the order of the A.O.U. Check-list (1957), except where it seemed more reasonable to group species by other criteria. The frontispiece should be consulted for both the geographic location of the stands, and other pertinent references to birds of aspen forests.

The methods of this study limit the usefulness of observations on larger species. Goshawks, *Accipiter gentilis*, Cooper's Hawks, *A. cooperi*, Red-tailed Hawks, *Buteo jamaicensis*, Broad-winged Hawks, *B. platypterus*, Prairie Falcons, *Falco mexicanus*, and American Kestrels, *F. sparverius*, were recorded. Flicker holes in aspen trees are important for nests of American Kestrels, but nests were not found in forests sampled. Only the Broad-winged Hawk in the parkland was found regularly nesting in forest areas, although Red-tailed Hawks commonly nest in aspen groves in both regions.

Great Horned Owl, *Bubo virginianus.*—Bred in all parkland and three Wyoming stands.

Long-eared Owl, *Asio otus.*—Bred in aspen forest, both regions.

Smaller owls.—Status not known.

Ruffed Grouse, *Bonasa umbellus.*—Bred in all parkland and three Wyoming stands.

Blue Grouse, *Dendragapus obscurus.*—Transient in New Mexico and Arizona stands.

Turkey, *Meleagris gallopavo.*—Transient in Arizona stands, early May in deep snow.

Lesser Yellowlegs, *Tringa flavipes.*—Bred in stand 35 in trees on pond edge.

Mourning Dove, *Zenaida macroura.*—Bred only in dense edges, both regions.

Black-billed Cuckoo, *Coccyzus erythropthalmus.*—Bred in aspen, parkland foothills to Wisconsin (Beals 1960; Bird 1961).

Broad-tailed Hummingbird, *Selasphorus platycerus.*—All mountain stands except Wyoming, California. Abundant, Utah and Colorado. Breeding was not confirmed, but evidence from Linsdale (1938), Woodbury and Sugden (1938), Bent (1940), and Grant & Grant (1968), makes this likely; two species of shrub and numerous flowers abundant and frequently used.

Calliope Hummingbird, *Stellula calliope.*—Stand 17 in Utah. Recorded in Wyoming aspen forests (Salt 1957).

Ruby-throated Hummingbird, *Archilochus colubris.*—Parkland only. Status not known.

Common Flicker, *Colaptes auratus.*—Lower frequency and abundance in parkland than mountains. Prefers to nest in larger trees (mean dbh 15.7 inches) than are common in parkland; possibly more important, they seemed to avoid dense ground cover (Short 1965), which is common in parkland but not in mountains. Prefer aspen over other forests types in northern Wisconsin (Beals 1960), and this tree species important to maintenance of large populations of *C. auratus cafer* in upland mountains. Zone of hybridization between *auratus* & *cafer* in foothills transition zone in parkland (Short 1965).

Pileated Woodpecker, *Dryocopus pileatus.*—Bred throughout parkland and one resident recorded in foothills stand 28, south of known range. Not known whether they peacefully co-exist with flickers (Schemnitz 1964) or come in conflict (Hoyt 1948, 1957).

Yellow-bellied Sapsucker, *Sphyrapicus varius.*—Subspecies *varius* in parkland, where species most abundant; *nuchalis* throughout mountains except California where *dagetti* recorded. Subspecific status in stands 28, 29, 31 not determined. Has been considered absent or rare in that area, not studied by Howell (1952). Salt and Wilk (1966) indicate that *varius* occupies most of that area. Possible recent colonist in newly matured aspen habitat since cessation of prairie fires (Andy Russell, personal communication, 1969), *S. v. varius* & *nuchalis* show strong preference for nesting in aspen trees (Howell 1952; Lawrence 1967) and their ranges may now meet near stand 30.

Small amount of interbreeding between *varius* & *ruber* in area of contact in northern British Columbia (Howell 1952) may have additional explanation: aspen may have only recently replaced conifers over large part of region when conditions favored fire (Wells 1970). Therefore only recent contact of *varius* with more sedentary *ruber.*

Causes of greater frequency and abundance of sapsuckers in parkland: occurrence of a few preferred *Betula* sapwell trees; parkland aspen wood easier to excavate due to its more rapid growth and higher disease frequencies than in mountains; no evidence of greater role of interspecific competition over holes between regions.

Hairy and Downy Woodpeckers, *Dendrocopus villosus* and *D. pubescens.*—Former had same frequency of abundance in two regions while latter occurred most often in parkland (Table 2). The four woodpeckers select trees on basis of size (Table 3), qualities of wood, bark, and exposure (Lawrence 1967), in contrast to cavity dependent species (Table 3). Smaller average tree size and earlier decay of aspen in parkland might be related to increased frequency of *D. pubescens.* The distribution of aspen and the range of Downy Woodpecker (Pitelka 1941) suggest that this tree is important to the species.

Eastern Kingbird, *Tyrannus tyrannus.*—Three stands in Alberta and Saskatchewan; two nests located 30 and 40 feet up in aspen trees in junction of main branches of crown, not typical (Davis 1941, 1955; Bent 1942).

Great Crested Flycatcher, *Myiarchus crinitus.*—Three stands, 37 at Paynton Saskatchewan most western. Most common, Good Spirit Lake, Saskatchewan. Spreading northwest (Houston and Street, 1959), possibly with post fire maturation of aspen trees providing nest sites. Species increases in numbers as aspen matures in Minnesota (Hickey 1956), and prefers climax forest farther east (Beals 1960).

Empidonax spp.—Collections not made. Evidence from Tatschl (1967), Hubbard (1965) and Johnson (1963) suggest that in the xeric and almost shrubless aspen forests of the south and central Rocky Mountains, most were Western Flycatchers, *E. difficilis.* In the single California stand and in Wyoming a different species predominated and was twice as abundant as in more southerly stands. Salt (1957) recorded the Willow Flycatcher, *E. traillii* in riverbottom aspen groves on the Snake River in Wyoming. In the upland aspen forest of the same area, stands 20–27, the birds were probably Dusky Flycatchers, *E. oberholseri,* in the more open, and Hammond's Flycatchers, *E. hammondii,* in the cooler shady habitats (Johnson 1963).

Least Flycatcher, *Empidonax minimus.*—The only small flycatcher recorded in the parkland except in stands 28 and 29 where the second and less common was probably *E. oberholseri.* This latter also in Cypress Hills aspen forest (Halladay 1965) where *minimus* is rare. Densities of *minimus* in parkland high, supporting contention that aspen forest is the most suitable habitat (MacQueen 1950). My census in wet year, 1969; large reductions can occur in dry years (Walkinshaw 1966). Drought intolerance of *minimus* may be additional evidence of its close relation to *hammondii* which selects shady cool habitat in the west (Johnson 1963).

Empidonax not recorded in Yukon aspen (Drury 1953), and *minimus* not common in northwest British Columbia (Rand 1944). Abundance of *minimus* differing between Minnesota (Kendeigh 1956) and Apostle Island (Beals 1960) aspen forests.

Western Wood Pewee, *Contopus sordidulus.*—More abundant in western mountains; parklands race different (Behle 1967). Possible competitive exclusion with Least Flycatchers (Kendeigh 1956) but parklands have fewer nest sites for Western Wood Pewee (see page 24, and Walkinshaw 1966), except stand 35 where pewees and Least Flycatchers both abundant. Absence of Western Wood Pewees in stands 28, 34, 36, 37, 38, 40, 41 suggests a difference in habitat selection from populations in mountains.

Tree Swallow, *Iridoprocne bicolor.*—Frequent and abundant in mountains, except Arizona; nearly absent in parkland forests and in more eastern aspen forests. Available holes not colonized in contrast to Chapman's findings (1955). Possible historical causes discussed page 39, but large number of holes in telephone poles of parkland (Bird 1961) may affect habitat selection.

Violet-green Swallow, *Tachycineta thalassina.*—Abundant in Arizona and Utah, present in Colorado, absent in Wyoming aspen forest. Exceptional numbers with Tree Swallows and Purple Martins, *Progne subis,* in Utah stands 15 and 16.

Purple Martin, *Progne subis.*—Nesting at 8,000 feet in Utah. Evidence from Behle (1968), Huey (1936) and Bird (1961) indicate importance of woodpecker holes in west. Exclusive use of martin houses in east attributed to loss of primary forest (Allen & Nice 1952), but may also have been influenced by slow change in nesting colony tradition and presence of introduced competitors in the east.

Steller's Jay, *Cyanocitta stelleri.*—Present in three stands but not breeding there.

Black-billed Magpie, *Pica pica.*—Recorded only in Wyoming and parkland where nests along rivers and near ponds.

Raven, *Corvus corax.*—Occassional both regions. Nests common in Wyoming aspen groves.

Common Crow, *Corvus brachyrhynchos.*—Recorded near one Wyoming and one parkland stand.

Black-capped Chickadee, *Parus atricapillus.*—Common in upland aspen forests of mountains; not restricted to streamside broadleaf habitats as for Dixon (1961) and Stefanski (1967). Most numerous and frequently encountered in Wyoming and parkland. Lower frequency of occurrence south of Wyoming may be related to greatly lessened importance of shrubs and thus volume of woody canopy (Sturman 1968a). Absent in Arizona and New Mexico stands. Occurs with Boreal Chickadee, *Parus hudsonicus,* during breeding season in aspen forests in northern British Columbia (Rand 1944; Munroe & Cowan 1947) and Yukon (Drury 1953), but there are fewer other arboreal birds, somewhat as for tits in Europe (Sturman 1968b). If *P. atricapillus* restricted to west in pre-Wisconsin time (Brewer 1963), aspen forests were major corridor for exchange to east.

Mountain Chickadee, *Parus gambeli.*—Transient in early May in stands in Arizona and New Mexico, although common and breeding in surrounding coniferous forests and mixed aspen-conifer (Steve Carothers, personal communication 1969, and John Tatschl, personal communication 1969). Therefore, no chickadees in those forests, contrary to the findings of Linsdale (1938) in the Toyabe mountains, Nevada. Large pure blocks of deciduous forests may be unsuitable to *gambeli,* and too isolated and southerly for *atricapillus.* Other areas provide interspecific contact (Orians & Wilson 1964), and chickadees have been recorded absent in appropriate eastern habitats (Brewer 1963).

White-breasted Nuthatch, *Sitta carolinensis.*—Appeared to be breeding in stand 1 only, which was near to *Pinus ponderosa* forests, the common habitat of the bird in the west (Bent 1948, Stallcup 1968). Also occurs in aspen forests in the east (Beals 1960).

Pygmy Nuthatch, *Sitta pygmaea.*—Appeared to be nesting near top of large, dead aspen, stand 3. Foraged in aspen and especially in few pines scattered in and to one side. This species rather intolerant of chickadees (Norris 1958) that were missing only in the aspen forests of the southwest.

Red-breasted Nuthatch, *Sitta canadensis.*—Appeared to be nesting in pure aspen of foothills and near some parkland stands that were up to 100 miles (161 kilometers) from nearest conifer forest.

House Wren, *Troglodytes aedon*.—More abundant in parkland although probable that nest cavities more abundant in mountains. Possible greater competition for nest cavities in mountains (Kendeigh 1941b; Allen & Nice 1952; Chapman 1955; Erskine 1964). Mean nest height lower than for other species (Table 3) except flickers. Careful nest placement can reduce competition (Thomas 1946). House Wren is absent or not important in more eastern aspen forests (Kendeigh 1956; Beals 1960); nor is it common in the Peace River Parklands (Munro & Cowan 1947).

Catbird, *Dumetella carolinensis*.—Four parkland stands.

Brown Thrasher, *Toxostoma rufum*.—Common in edges.

American Robin, *Turdus migratorius*.—Inexplicably unimportant or absent only in Saskatchewan and Manitoba stands. Found in aspen forests from Yukon (Drury 1953) to Wisconsin (Beals 1960).

Hermit Thrush, *Catharus guttatus* and Veery, *C. fuscesens*.—Recorded together only twice (33, 37). Veery more abundant, especially in the two foothills stands outside the range of the Hermit Thrush (Dilger 1956), but dense shrub and forb layer on moist soils especially favorable there. Hermit Thrush prefers edges within forest, is more tolerant of dry habitats; found throughout mountains except Wyoming near edge of range (Dilger 1956); both species in more eastern aspen (Beals 1960) but in pure aspen forests only the Veery occurred (Beals personal communication 1970; Kendeigh 1956; Hickey 1956). Hermit and Swainson's Thrush, *C. ustulatus* occur in Peace River Parklands (Munroe and Cowan 1947) and Yukon aspen forests (Drury 1953). Varied Thrush, *Ixoreus naevius* in heavy poplar forests of Liard River (Rand 1944).

Mountain Bluebird, *Sialia currucoides*.—Abundant in mountains and absent in parklands as discussed p. 40. Criddle (1927) found it only in open sites in Manitoba, whereas it nests deep within aspen forests in mountains. Range extension east in parkland aided by holes in posts, poles and later, nest boxes (Criddle 1927) resulting in interbreeding with, and replacement of *Sialia sialis* (Lane 1968). Eastern Bluebird is not a component of more eastern aspen forests.

Western Bluebird, *Sialia mexicana*.—Nested in equal numbers with Mountain Bluebird in three stands at Hart Prairie, north of Flagstaff, Arizona, with some strife. Usual altitudinal separation (Bent 1949) may be lacking here due to nearby Ponderosa Pine forests, which are absent or scarce over a large part of the central Rocky Mountains (Daubenmire 1943). Tatschl (1967) records both together in New Mexico.

Townsend's Solitaire, *Myadestes townsendi*.—Breeding in two stands located near suitable nest ledges (Peabody 1935; Paul 1964).

Cedar Waxwing, *Bombycilla cedrorum*.—Present in most parkland stands in June with nest building in some in canopy in July. Observed only once in mountains (16 June 1966, stand 27). More open aspen forests (Lea 1942) with berry producing shrubs (Putnam 1949) probably good habitat. Not in more eastern aspen forests, but this and Bohemian Waxwing, *Bombycilla garrulus*, appear to breed in Peace River Parklands (Munro and Cowan 1947).

Starling, *Sturnus vulgaris*.—Nested in cavity at top of large aspen; 8,000 feet, Wasatch Plateau, central Utah. Apparently new record (Kessel 1953; Bailey 1966). Not breeding in any parkland stands, but present in region since 1934 (Bird 1961; Myres 1958).

Warbling Vireo, *Vireo gilvus*.—The most abundant and frequently encountered bird in aspen forests throughout western mountains; abundance greatly reduced, less frequently encountered in parkland (Table 1).

Red-eyed Vireo, *Vireo olivaceous*.—Found only in parklands; similar abundance to

Warbling Vireo. Combined abundance did not always equal that of *V. gilvus* in mountain stands. Hamilton (1959, 1962) believed these two closely related species were laterally or altitudinally separated where sympatric. No vireos recorded in Yukon aspen groves, but four warblers recorded (Drury 1953). Only Red-eyed Vireo in pure aspen of Apostle Islands, northern Wisconsin (Beals 1960).

Abundance of the Red-eyed Vireo in parkland stands appears lower than expected (Lawrence 1953; Southern 1958; Kendeigh 1948), suggesting some mutual exclusion. Small difference in habitat use may be important, such as nest height and foraging level (Lawrence 1953; Bent 1940). Red-eyed Vireo requires a shrubby stratum or thicket of young trees (Lawrence 1953) but Warbling Vireo numbers not reduced in shrubless aspen forests in western mountains. Highest combined densities for these species occurred in stands 39 and 40 where the trees were tall and the shrub-layer very dense.

Red-eyed Vireo may benefit from slightly earlier arrival (see Howell 1952). Vertical differences in nesting and feeding activity should be measured and compared between areas; influence of other species such as orioles should be considered, as should hunting strategies. Success of each species must also be measured during breeding.

Orange-crowned Warbler, *Vermivora celata.*—Recorded once on territory in Glacier County Montana aspen forest on 12 May 1969. Common in aspen of nearby Cypress Hills (Halladay 1965; Bird and Halladay 1967).

Yellow Warbler, *Dendroica petechia.*—Totally absent in dry shrubless aspen forests of southern and central rocky mountains except for one very mesic, shrubby forest in Colorado. Common in Wyoming and parklands stands. Recorded in some midwestern aspen (Hickey 1956; Fashingbauer et al. 1957) and not in others (Beals 1960; Kendeigh 1956). Not recorded for Yukon aspen forests (Drury 1953), but present in parkland in British Columbia (Munro & Cowan 1947). Near surface water, density increased with shrub cover (Fig. 47). Female shows preference for territories with shrubbery (Ficken and Ficken 1966), older shrubs providing the best nest sites (Kendeigh 1941a); trees important singing posts for males (Kendeigh 1941; Morse 1966). Montane Yellow Warblers may be adapting differently (Salt 1963).

Audubon's Warbler, *Dendroica coronata audubonii.*—Common in pure aspen forests of western mountains; not dependent on conifers contrary to Hubbard (1969); absent in California, where Pacific race may prefer conifers (Bent 1953). Absent in foothills of parklands and without an obvious replacement. Occurs near foothills stands, and stands 29 and 30 are in zone of introgression for *audubonii* and *coronata* (Hubbard 1969). Present in Cypress Hills aspen woods (Bird and Halladay 1967). Additional vireos and abundance of flycatchers may be factors in the absence of a *Dendroica* in parklands. Myrtle Warbler, *D. c. coronata,* common in Yukon aspen groves (Drury 1953).

Ovenbird, *Seiurus aurocapillus.*—In parkland stands irregularly as far south as Millarville, Alberta (S.W. of Calgary), somewhat beyond recorded breeding range (Salt & Wilk 1966). Possibly breeds in region of Waterton Park, Alberta (Andy Russell, personal communication 1969). More mesic aspen forests in Boreal region apparently better habitat; abundance in stand 34 two times greater than in parkland stands, where it is also less frequently encountered. Weatherill and Keith (1970) found the Ovenbird abundant in 19 aspen forests plots in the region of stand 34. Michigan hardwood forests (Hann 1937), one pair per three acres; parkland stands below this level, boreal stands above it. Stenger & Falls (1959) found territories smaller in open stands than other forests. Periodic summer drought and daily desiccation of litter in parkland probably provide less favorable conditions for feeding requirements (see Hann 1937;

Bent 1953; Stenger 1958). Not present in Yukon aspen groves (Drury 1953), but abundant in aspen on islands, northern Wisconsin (Beals 1960).

Connecticut Warbler, *Oporornis agilis.*—Bred in parkland on Eagle Hill, Alberta, 150 miles (241 kilometers) north of range of MacGillivray's Warbler, *O. tolmiei,* and in Peace River Parkland where the two species may occur together (Munro & Cowan 1947). Found on territories in aspen adjacent to five stands as far east as Good Spirit Lake, Saskatchewan. Most males appeared widely dispersed from each other except at Good Spirit Lake, where several were found in 20 acres. Species not rare as stated in Griscom and Sprunt (1957), but widely dispersed and locally more common as described by Bent (1953) and Salt and Wilk (1966).

Mourning Warbler, *Oporornis philadelphia.*—Only a single male recorded, in two eastern parkland stands (39, 40). Common in shrubby aspen forest farther east and south (Kendeigh 1956; Beals 1958, 1960; Cox 1960). Appears to prefer more moist conditions than Connecticut Warbler (Bent 1953). Increased shrub cover favorable (Beer 1958).

MacGillivray's Warbler, *Oporornis tolmiei.*—Present in three mountain stands with four pairs in one shrubby, mesic, north facing stand. Salt (1957) recorded it in Wyoming aspen forests. Not found in any xeric, nearly shrubless stands in southern mountains where it has been recorded in better habitat (Miller 1934; Phillips 1947). Also occurs in region of foothills parkland (Phillips 1947; Salt and Wilk 1966), and aspen of Cypress Hills (Bird and Halladay 1967).

American Redstart, *Setophaga ruticilla.*—One stand in each of Prairie Provinces; abundance low. Occurs in high densities in more eastern deciduous forests (Hickey 1940; Griscom and Sprunt 1957). Wide vertical range for feeding (Ficken 1962), nesting (Ficken 1964) and importance of flycatching (Ficken and Ficken 1962) suggests ecological similarities to Audubon's Warbler, common in the western aspen forests.

Baltimore Oriole, *Icterus g. galbula.*—Common species of parkland, abundance correlated with canopy height (Fig. 19, 20). Uncommon in foothills region and absent farther south in uplands and Cypress Hills. Not replaced in mountains by *I. g. bullockii* (Beecher 1950; Sibley and Short 1960). Baltimore Oriole uncommon (Beals 1960) or absent (Kendeigh 1956; Fashingbauer et al. 1957) in more eastern aspen forests. Also uncommon northwest of Edmonton Alberta (Soper 1949) and not found in Peace River Parklands (Munro and Cowan 1947).

Western Tanager, *Piranga ludoviciana.*—Present in some western aspen forests and stand 28 in foothills but not replaced in parklands by Scarlet Tanager, *P. olivacea,* until Minnesota (Kendeigh 1956; Fashingbauer et al. 1957). Possible relationship to abundance of orioles in parkland?

Brown-headed Cowbird, *Molothrus ater.*—More abundant and frequently encountered in parkland than mountains; most abundant in stand 35 where small herd of *Bison bison* frequently encountered. Interspersion of forest, prairie, meadow and cultivated land in parkland provides ideal habitat (Mayfield 1965), furthered by extension of agriculture northward in recent years (Bird 1961) enabling contact with forest species such as Mayfield (1965) has described for the east.

Recent impact of cowbird on forest species (Mayfield 1965) in northern parkland may be important, being additional to historical factors. Could have differential impact on species abundance such as between Warbling and Red-eyed Vireos, affecting coexistence. Lower abundance of cowbirds in montane stands may be partly related to better adaptions of host species though long association (Mayfield 1965) if montane aspen forests have been closely associated with meadows and grassland for long periods.

Black-headed Grosbeak, *Pheucticus melanocephalus.*—Characteristic though not abundant species of western aspen forests. The range of the closely related Rose-breasted Grosbeak, *P. ludovicianus*, in prairie provinces is defined on north and west by the extent of aspen parkland (West 1962), but it does not extend north of the Peace River (Munro and Cowan 1947). Shrubby parkland forests support higher populations than western mountains (Fig. 45, 46), but both species commonly foraging in canopy as Dunham (1966) found. Both occur in Cypress Hills (West 1962), but in Alberta parkland their ranges are separated, although the habitat is now continuous, this fact having apparently historical explanation (p. 77). Therefore foothills parkland may become another region of interbreeding.

Lazuli Bunting, *Passerina amoena*.—Pair in open shrubby stand (18) with southwestern exposure, similar to situation recorded by Salt (1957) for Wyoming, and for foothills on edge of stand 28. Most aspen stands too mesic and closed for this species.

Purple Finch, *Carpodacus purpureus*.—Presence unusual and associated with some planted spruce near stand 39 (Salt and Wilk 1966; Bent 1968).

Cassin's Finch, *Carpodacus cassinii*.—Breeding in many western mountain stands regardless of presence or absence of conifers. Nests built in tree crowns. Absent in southern Rocky Mountain stands.

Evening Grosbeak, *Hesperiphona vespertina*.—Breeding in three Arizona stands and abundant in area in 1968. Nests located high in canopy of aspen trees and in isolated Ponderosa Pines.

Pine Siskin, *Spinus pinus*.—Breeding not confirmed but frequently encountered in May, June and July in pure stands from Arizona to Alberta foothills. Flocks of this early breeder (Bent 1968) slowly increased up to dozen birds in late June and July. Could have nested in deciduous trees (Bent 1968) or used scattered conifers, in a few stands.

Common Goldfinch, *Spinus tristis*.—Small numbers throughout parkland; one nesting pair in Wyoming. Riparian woodland preferred in west (Coutlee 1968), including aspen (Salt 1957). Edges and aspen groves preferred in parkland (Bird 1961). This late breeding species (Stokes 1950) often nests in loose aggregates (Berger 1957) with thistle, *Cirsium* spp., as an important component of nesting habitat. Aspen forests appear not well suited. Not recorded in more eastern aspen forests, and is not common to the northwest of parkland (Munro and Cowan 1947).

Green-tailed Towhee, *Chlorura chlorura*.—Nesting in edges, shrubby upland aspen forests.

Rufous-sided Towhee, *Pipilo erythrophthalmus*.—Two stands in eastern parklands and near a few others to west. Also in more eastern aspen (Beals 1960) and Cypress Hills (Bird and Halladay 1967).

Juncos, *Junco* spp.—Every stand in mountains; abundance correlated with ground cover (Fig. 52). From Miller (1941), *J. caniceps dorsalis* in stands 1–5; *J. c. caniceps* in stands 6–18; *J. hyemalis thurberi* in stand 19; *J. h. mearnsi* in stands 20–27. No stand was located in a zone of hybridization. Miller (1941) recorded all but *thurberi* in pure aspen forests. No juncos recorded in foothills or parkland stands, although *montanus* and *hyemalis* occur in foothills regions and *mearnsi* occurs in the Cypress Hills, aspen groves. Juncos also absent in "the true parklands of Grand Prairie, Spirit and Peace Rivers" (Soper 1949). *J. h. hyemalis* occurs in aspen groves in the Yukon (Drury 1953).

White-throated Sparrow, *Zonotrichia albicollis*.—Bred commonly in parkland stands from Olds, Alberta, but absent in foothills. Strong preference for aspen forest (Beals 1960).

White-crowned Sparrow, *Zonotrichia leucophrys*.—Bred in seven montane and two foothills stands with many pairs well within forests of mature, large, well-spaced trees. Large populations in three Utah stands. Large gap between ranges of *leucophrys* and *albicollis* in aspen of Alberta.

Chipping Sparrow, *Spizella passerina.*—More abundant and commonly encountered in mountains than parkland. Greater shrub cover in parkland reduced number of open areas favored for feeding; also rather similar to next species.

Clay-colored Sparrow, *Spizella pallida,* present in parkland forests. This and last species present in Peace River Parklands (Munro and Cowan 1947), but the latter not in Yukon aspen groves (Drury 1953). Neither in more eastern aspen forests.

Lincoln's Sparrow, *Melospiza lincolnii.*—One pair in a Utah stand encompassing a wet grassy area with a few shrubs around a small spring near edge.

Song Sparrow, *Melospiza melodia.*—Both regions, always with surface water nearby. Highest densities where large, well spaced trees occurred with moderate shrub cover. Beals (1960) found strong preference for aspens.

SUMMARY

Aspen (*Populus tremuloides*) often occurs in essentially pure stands at mid-altitudes throughout a large portion of the western mountains of the United States, and at lower elevations in the Canadian parkland and mixed boreal forest. Quantitative measurements of the breeding bird populations in homogeneous aspen forests were made using a strip census method in 41 forests from Arizona to Wyoming and from southwestern Alberta to Manitoba. Tree density, diameter, tree height and crown thickness, and shrub and ground cover were estimated from circular quadrats.

The number of species of birds and their relative abundance was found to decrease in a similar pattern in the montane and parkland regions as tree density increased or average tree diameter decreased. The total number of breeding species or individuals was usually highest in parkland forests.

Tree density, canopy height, and canopy thickness were found to be correlated with the abundance or number of species of birds arranged or grouped by the nature of their exploitation of the canopy. There were often more species of flycatching birds in montane forests, but the number of individuals was greater in parkland forests where the Least Flycatcher (*Empidonax minimus*) was abundant.

The number of hole nesting species and their relative abundance was found to be roughly correlated with tree density and average tree diameter, but was highly variable. Although the maximum number of woodpeckers in mature forests was the same in both regions, woodpecker populations were higher in parkland forests of high tree density than in similar montane forests. The number of cavity dependent birds is somewhat related to the number of hole digging birds in a forest. At similar tree densities, parkland forests have fewer species and numbers of cavity dependent birds than do montane forests.

The abundance of woodpeckers in younger, denser forests in the parkland compared to similar forests in the mountains may be related to the faster

growth and greater infection by disease of the parkland tree trunks, rendering them easier to excavate. The variability in relative abundance and number of species of hole nesting birds in similar mature forests in both regions appears to be related in part to differences in tree health. The lower populations of cavity dependent birds in parkland aspen forests is probably the result of the shorter life of these forests and their greater historical instability.

The number of birds nesting in shrubs in both regions increased as total understory cover (shrubs, grasses, and forbs) increased. In the mountains but not in the parkland the number of birds nesting on the ground decreased as percent cover of litter increased, while birds feeding on the ground, in both regions, decreased as percent cover of litter increased.

Although the total number of individuals and species of birds in most parkland forests is greater than in montane forests, species diversity (H′) is very similar in both regions. The lower H′ values per number of species in the parkland is partly related to habitat instability. H′ is as high in montane aspen forests lacking shrub cover as in the shrubbiest parkland forests. The H′ value of a single aspen forest located well within the boreal region north of the parkland was the lowest value recorded in any mature forest. Its low bird species diversity is due to the absence of a number of bird species, and descriptions in the literature confirm the probability of a rather abrupt drop in bird species diversity throughout northwestern boreal aspen forests, which are structurally similar to those farther south.

The avian species composition of montane aspen forests has been more influenced by surrounding habitats than has the composition in parkland forests, and there are strong affinities and resemblances to eastern deciduous forests in both regions. This may be related to the history of *Populus tremuloides* since the Pliocene. Historical and ecological factors may result in some communities in all three regions being unsaturated with bird species on the basis of structural features of the forest.

Individual bird species are discussed in relation to all of the above problems. Many species show strong preferences for aspen trees or forests as nesting habitat.

ACKNOWLEDGMENTS

I would like to thank Edward Beals for his encouragement and direction during the study and for criticizing many drafts of the dissertation. John T. Emlen was most helpful in the early stages of the study and my later discussions with him were valuable. The criticisms and suggestions of W. G. Reeder, O. L. Loucks and Mike Roberts were most helpful. My fellow graduate students on the "fourth floor" provided stimulating criticisms throughout the study. A. A. Beetle of the University of Wyoming helped stimulate my interest in aspen ecology.

I am indebted to Ann Scott for her assistance in the field in 1966; for their assistance at different times, I am grateful to Bill Anaka, Steve Carothers, Helmer Johnson, Bob Jones, Tracy Lang, W. B. MacDougall, Jerry Michalski, Andy and Ann Russell, Bob Scace, Steve Spondberg, Don Taylor, Barry Tether, and Deidrie Webb. For their hospitality while I was travelling and in the field, I wish to express my appreciation to L. Floyd Clarke and other members of the staff at the Jackson Hole Biological Research Station, and to Jerry and Sue Downhower, Walter Hughes, Stewart Raby, Mr. and Mrs. Andy Russell and Frank Switzer. I am indebted to numerous persons from the National Park Services of the U.S. and Canada, the U.S. National Forest Service, and Good Spirit Lake and Moose Mountain Provincial Parks, Saskatchewan.

Without the encouragement, criticisms, and assistance of Jean Richardson Flack the study could not have been conducted, and without Sarah Flack, it would have lacked a whole new dimension.

I gratefully acknowledge support from the Frank M. Chapman Memorial Fund, the New York Zoological Society, and the University of Wisconsin. Part of this work was done while I was on a National Science Foundation Traineeship. Final Revision was carried out while I was working for the New Zealand Wildlife Service.

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APPENDIX 1

STATISTICAL TREATMENT OF DATA FROM FIGURES 5, 6 AND 7

In order to determine whether there was a significant difference in diversity, or number of species or individuals between montane and parkland stands in figures 5, 6 and 7, a median test was used. Data in figures 5 and 7 were treated after rotating the axis of the points 45° clockwise. The distribution of points above and below the median was tested using Chi Square to determine if their was a significant departure from a 50-50 distribution. There was a highly significant difference (99.5% level) in figures 5 and 7 and a significant difference (97.5% level) for figure 6.

I am grateful to Mike Weiner for his help with these tests.

APPENDIX 2

AVIFAUNAL AFFINITIES

The absence of adequate fossil records, the long evolution, and the great mobility of birds make it necessary to use indirect means of tracing the history of local bird faunas (Mayr 1946). In many cases whole families may be assigned a single place of origin, while in others subfamilies, genera and species indicate secondary centers of evolution. These designations are based on present distributions and a few fossils. They should be accepted cautiously in view of the fact that the much better known fossil record of mammals shows repeatedly that many living orders and families originated in areas where none now survives. For this discussion we are primarily interested in knowing whether a species probably evolved in deciduous or broadleaved forests and colonized aspen forests from the south or east, or whether it evolved in coniferous forests and invaded from the north. Species in the Old World category are assumed to have had their origins in the Old World, their ancestors having crossed to the New World in coniferous forests on a Bering land bridge during the Pliocene or Pleistocene. The members of the New World group are assumed to have had their origins either in arcto-tertiary forests or tropical and subtropical habitats.

When those species found breeding in aspen forests throughout the mountains are grouped according to their origins, it can be seen that roughly 70 percent are of New World and 30 percent of Old World origin (Table 1). The New World element is even more strongly evident on the basis of abundance, but the stands in Arizona have the lowest New World affinities.

The avifauna of the parkland aspen, which contains a large component of species found in eastern North America, is somewhat more strongly New World in its affinities. The transitional foothills area is similar to the montane forests in its affinities. Deciduous forests from the east, while varying greatly in composition, also show strong New World affinities (Mayr 1946).

In contrast, species of birds breeding in climax coniferous forests in Colorado show strong Old World affinities, almost exclusively so on the basis of abundance of breeding pairs (Snyder 1950). In various forests in the Rocky Mountains, Snyder also found that as the coniferous elements of the vegetation increase (with altitude), so does the Old World element in the bird populations.

Forest species of New World origin therefore are most successful as a group using deciduous forest as their breeding habitat. This success suggests that these species or their progenitors have been closely associated with deciduous trees during at least their recent evolutionary history.

TABLE 1

AVIFAUNAL AFFINITIES*

Region	Total No. of species recorded	Old World	New World	% New World
Arizona	24	10	14	58
California	23	8	15	65
Utah-Colorado	31	9	22	71
Wyoming	25	8	17	68
Foothills	33	11	22	66
Rest of Parkland	37	9	28	75

* After Mayr 1946.

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