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Breeding Bird Populations and Habitat Utilization in Aspen Stands of Upper Logan Canyon

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BREEDING BIRD POPULATIONS AND HABITAT UTILIZATION IN ASPEN STANDS OF UPPER LOGAN CANYON

by

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of the requirements for the degree

of

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Breeding Bird Populations and Habitat Utilization

in Aspen Stands of Upper Logan Canyon

by

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Censuses of two 20-acre plots in upper Logan Canyon, Utah, were made by the spot-mapping method during 1970 and 1971 to determine the differences in composition and density of breeding-bird populations in aspen stands of significantly different density and stature. The less dense stand of greater average d.b.h., average height and per cent ground cover had 20 breeding species totalling 615 pairs per 100 acres (expressed as equivalent territories). The more dense stand of smaller trees and brushy undergrowth had 14 breeding species with 267.5 equivalent territories per 100 acres. Nine species were found on both areas. Observations of foraging height were made concurrently with recordings of time spent at various methods of feeding- ground, foliage, bark, hover, and hawking- for the birds of the more open stand. Comparison showed that more ground- and low bush-nesters were present on the dense, brushy stand whereas more cavity-nesters were found in the larger trees. Cavity excavation was limited to trees of greater d.b.h. and cavity-dependent birds were thus limited by nest-hole availability. The horizontal, heavy branch stubs preferred by pewees and tree swallows and the high perches and open areas of the olive-sided

flycatcher were also limited to the less dense stand. Cassin's finches and pine siskins were not found in the dense stand which had fewer invading conifers and was farther from conifer stands. Attributes of the terrain, foraging sites, nest sites, and location of perches were analyzed as possible proximate factors of habitat selection within aspen.

(45 pages)

INTRODUCTION

This study was designed to determine the habitat preferences and population densities of birds breeding in aspen in northern Cache County, Utah. Field work was conducted in upper Logan Canyon in two aspen stands of significantly different density and stature. Comparisons between breeding populations were based upon censuses taken in 1970 and 1971. The zones within the habitat utilized by particular species and the methods of foraging used by those species were determined quantitatively. Attributes of the terrain, foraging sites, nest sites and location of perches were analyzed as possible proximate factors of habitat selection (Hildén, 1965).

STUDY AREAS

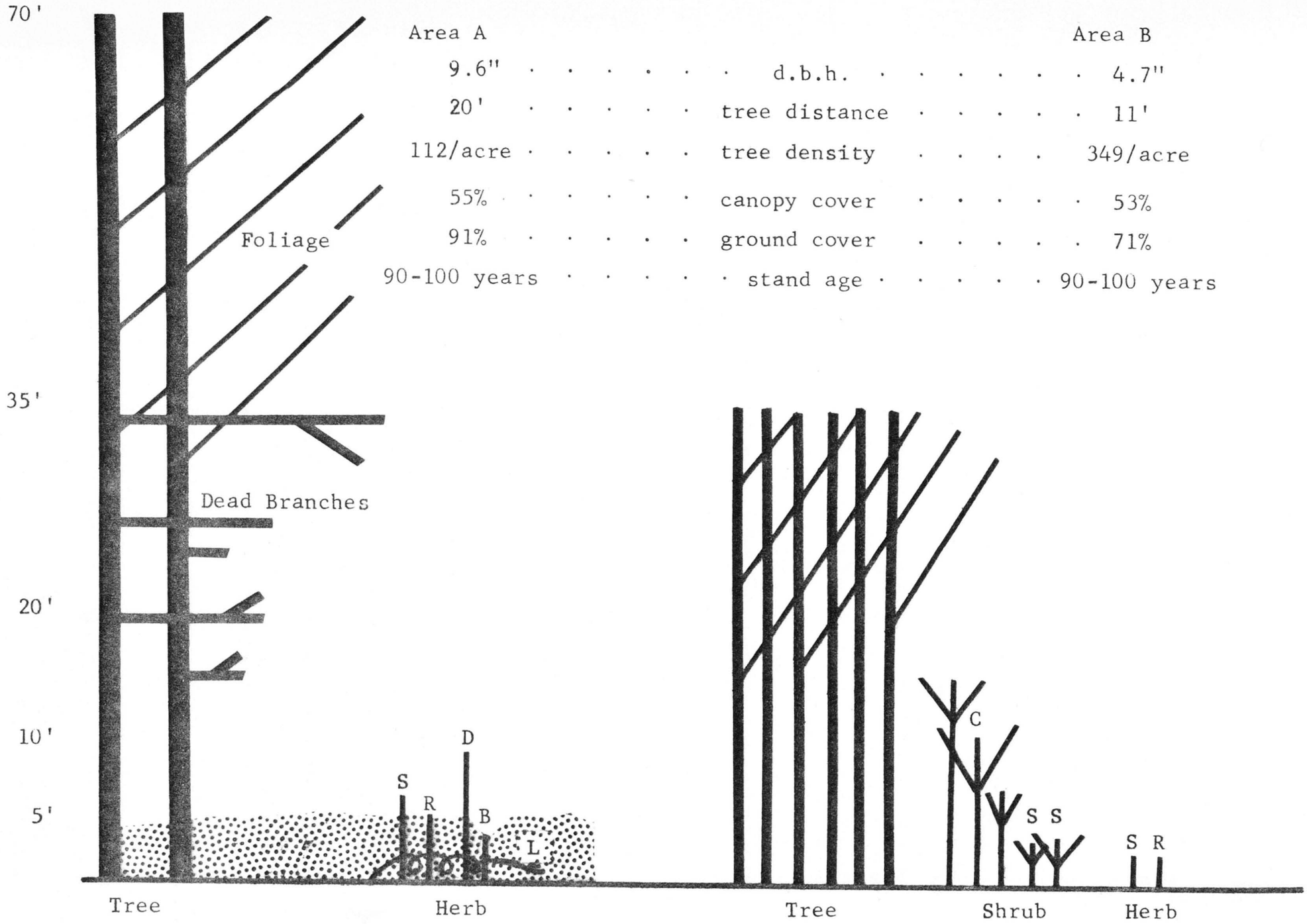
The two study plots of 20 acres each were established in upper Logan Canyon, Cache County, Utah. Area A, the stand of tall trees, was located 3.3 miles north of highway 89 on the Franklin Basin road at the site of the Soil Conservation Service Klondike Narrows snow survey station (#147, Utah watershed research laboratory). Area B, the dense stand of small trees was 2.8 miles NW of the highway, and to the north of the Logan River. This locality was 21 airline miles NNE of Logan, township 14 N, range 3 E, section 10 (area A), section 14 (area B), Salt Lake Meridian. Area A was at the base of a north-facing slope at 7420 ft (2263 m) elevation. This was a closed aspen forest with openings created by the death of old trees, and by a dirt road and the half-acre weather station (not included in the censuses). Structurally there were two vegetational layers: tree and herbaceous. The 5-foot herbaceous undergrowth was dominated by Senecio serra, Rudbeckia

occidentalis, Delphinium occidentale and grasses of which Bromus marginatus was dominant. Lathyrus pauciflorus filled in the area between the above species. A complete description is given by Holman (1973). The large trees reached a height of 65-70 ft and had extensive horizontal dead branches below the foliage.

Area B was located on a SSW-facing slope at about the same elevation, across the Logan river and 0.8 miles from area A. The vegetation formed three layers: tree, shrub, and herbaceous. The aspens were small in diameter, reached a height of 35 ft, and formed a dense grove. The shrubs included sagebrush (Artemisia) and snowberry (Symphoricarpos) near the periphery and chokecherry (Prunus virginianus) more central on the plot. The herbaceous layer was dominated by Senecio serra, Rudbeckia occidentalis and grasses but did not form a continuous mat. There was 71 per cent green ground-cover as compared to 91 per cent for area A. The age of both stands was 90-100 years and the ring data showed that aspen growth correlated with mean annual precipitation with a faster rate of growth on area A (Jan Henderson, pers. com., April, 1973). The vegetational structure for the two areas is shown in fig. 1 and the aspen characteristics are compared in table 1.

METHODS

Two 20-acre plots were selected for uniformity of aspen. Each plot was marked out in quarter-acre sections with the use of compasses and measured string lengths to facilitate censusing. The tree nearest each grid stake was banded with forester's tape and marked with a letter and a number to designate its relative position along the width and length of the plot. The territory mapping method of Williams (1936) was used to determine the distribution and number of birds on the areas. The



Area A		Area B
9.6"	d.b.h.	4.7"
20'	tree distance	11'
112/acre	tree density	349/acre
55%	canopy cover	53%
91%	ground cover	71%
90-100 years	stand age	90-100 years

FIGURE 1. Vegetational structure for the two study plots. (S= Senecio, R= Rudbeckia, D= Delphinium, B= Bromus, L= Lathyrus, C= chokecherry, S S= sagebrush and snowberry).

TABLE 1. Vegetational comparison of study plots A and B.

	Area A	Area B
Avg. distance between living aspen (ft)	20	11
Avg. d.b.h. of living aspen (in)	9.62	4.74
Living aspen per acre (density)	112	349
Basal area per tree (sq ft)	.557	.145
Total basal area per acre (sq ft)	62.46	50.62
Dead snags per acre	17	—[a]
Dead trees per acre	12	—[a]
Subalpine fir per acre	3	<.5
Douglas-fir per acre	0	<.5
Percent canopy cover	55%	53%
Percent ground cover	91%	71%
Overstory height (ft)	60-70	35
Average age of aspen (yrs)	90-100	90-100

[a] Indicates not measurable.

positions and movements of all birds were recorded on mimeographed maps as the observer walked slowly along alternate grid lines 209 ft apart. Each census required about three hours to complete. The route of censusing followed one day was reversed the next time on the same plot for equable observation of all sections. A system of abbreviations for the species names was used to facilitate rapid recording of data. The abbreviations were circled for birds sighted and a square drawn around the notation for estimates of a singing bird's location. A solid line was drawn between recordings of individuals of the same

species singing simultaneously. Special and persistent effort was made to discover nests. Censusing was conducted in the early morning (5:30, area A,1970, area A and area B, 1971) or evening (area A, 1970) when avian activity was greatest. Area A was censused 28, 29, 30 June and 1, 2, 3, 4, 9, and 10 July 1970 and 10, 17, 22, 23 June and 2, 13, 16, and 17 July 1971. Censuses were taken 7, 12, 19, 26, 29, 30 June and 6, 14, and 15 July 1971 on area B. Surveys for owls were made during February, March, and April, but no nests were found on or near either area. After each day's census the data collected were transferred to permanent summary sheets (color coded by day of census) for the individual species. Since most birds occurred more frequently in the vicinity of their nests, the summary sheets revealed clusters of observations on different areas of the grid. Estimates of the number of breeding pairs of each species were made from the occurrence patterns, location of specific nests and the simultaneous singing of two or more males. Estimates were expressed as the number of equivalent territories to account for birds active on the areas but with only parts of their territories within the study area proper.

Locations of foraging and other activities were quantified by measuring the percentage of total observed time each species occurred within specific zones of the environment. Zones for live aspen were the main trunk, upper branches, foliage and dead branches. Other zones recorded were stump, dead tree, fallen tree, rock, conifer and sapling (Stallcup, 1968). The distributions of feeding methods- ground, foliage, bark, hover, and hawking-(Crowell, 1962) and foraging stance were observed. Classification of stance included standing upright, hanging upside down and perching on a vertical surface (Sturman, 1968). The vertical distribution of activity was determined for strata of

0-½ ft, ½-6 ft, 6-15 ft, 15-30 ft, and above 30 ft. The substrate and stratum at which each timed activity occurred were recorded on a composite data sheet. A stop watch was used to measure the duration of each activity. Each observation was terminated when the bird changed its activity, was lost from sight or after ten minutes. Timed observations were made while the observer was randomly walking area A looking for nests and during the early morning hours on days when a census was not made. Timed observations totalled between 500 and 3,000 seconds for each species.

The point-centered quarter method (Cottam and Curtis, 1956) was used to analyze the aspen stands. The quarter-acre markers occurring within the plot proper were used as center points and the four quadrants were determined by the grid rows. The distance from the center point to the closest living aspen in each quarter was measured, and the d.b.h. (diameter breast height) for each tree was recorded. Fifty center points were used on each plot. The number of dead aspen trees, stumps and snags, and invading conifers were determined by actual count. To measure canopy and ground cover, an ocular tube was made by taping cross-threads across one end of a cardboard cylinder from a roll of bathroom tissue. A weight was suspended from the other end to help sight directly upwards. While taking ten paces into each quadrant from the center point, recordings were made on alternate steps giving 20 plus or minus readings for the presence or absence of canopy cover sighted where the threads crossed. Twenty plus or minus readings taken through the tube held at arm's length and pointed downward provided a record of the presence or absence of green vegetation on the ground. Fifty center-points were used on each area. The percentage plus recordings of the

total equals percent cover (James and Shugart, 1970). Tree ring data were obtained with increment borers to determine aspen ages. An Abney level was used to measure the height of trees.

AVIAN DENSITY AND COMPOSITION

A list of all bird species observed on the study areas during the breeding season and their status on each plot is presented in table 2. The scientific and English names used conform to the thirty-second supplement to the American Orithologists' Union check-list of North American birds (1973). A summary comparison of the avifaunas of the two aspen stands is shown in table 3. These tables show that only about one-third of the total species observed occurred on both areas. According to Bailey and Niedrach (1965), the ruffed grouse is an uncommon resident in the northern mountains of Utah and the orange-crowned warbler is a common migrant but uncommon breeder in the mountains. The other 23 species breeding in the aspens were rated as "fairly common," "common," or "abundant" in the summer in northern Utah. None of the breeding species observed are limited to aspens as a tree type. Most occur anywhere they find their specific requirements of deciduous trees, shrubs, streams, open spaces among trees of any type, or altitude. Audubon's warblers breed in the mountains of Utah from 7,000-10,000 ft and nest in almost any of the components of the forests within those altitudes; pine, fir, spruce, aspen, or oak (Bent, 1953). Orange-crowned warblers occur at 6,000 ft and above where dense willows, alders, aspens, and yellow pines all provide the proper habitat (Bailey and Niedrach, 1965; Bent, 1953). The black-headed grosbeak is a mountain breeder found in deciduous trees and bushes along streams (Bent, 1968) and the "normal habitat" of the broad-tailed hummingbird is close to mountain streams

TABLE 2. Bird species observed on the study areas during the breeding season.

Species	Status* Area A	Area B
Turkey Vulture (Cathartes aura)	V	—
Goshawk (Accipiter gentilis)	—	V
Sharp-shinned Hawk (Accipiter striatus)	V	—
Red-tailed Hawk (Buteo jamaicenses)	V	—
Swainson's Hawk (Buteo swainsoni)	V	—
American Kestrel (Falco sparverius)	V	V
Ruffed Grouse (Bonasa umbellus)	—	B
Great Horned Owl (Bubo virginianus)	V	V
Pygmy Owl (Glaucidium gnoma)	—	V
Common Nighthawk (Chordeiles minor)	V	—
White-throated Swift (Aeronautes saxatalis)	V	—
Broad-tailed Hummingbird (Selasphorus platycercus)	B	B
Rufous Hummingbird (Selasphorus rufus)	V	—
Red-shafted Flicker (Colaptes auratus cafer)	B	—
Yellow-bellied Sapsucker (Sphyrapicus varius)	B	—
Hairy Woodpecker (Dendrocopos villosus)	B	—
Downy Woodpecker (Dendrocopos pubescens)	V	—
Flycatcher (Empidonax sp.) [?Hammond's- hammondii]	B	B
Western Wood Pewee (Contopus sordidulus)	B	—
Olive-sided Flycatcher (Nuttallornis borealis)	B	—
Violet-green Swallow (Tachycineta thalassina)	B	—
Tree Swallow (Iridoprocne bicolor)	B	—
Purple Martin (Progne subis)	V	—
Steller's Jay (Cyanocitta stelleri)	V	V
Black-capped Chickadee (Parus atricapillus)	V	B
Red-breasted Nuthatch (Sitta canadensis)	V	—
House Wren (Troglodytes aedon)	B	B
American Robin (Turdus migratorius)	B	B
Hermit Thrush (Hylocichla guttata)	—	B
Mountain Bluebird (Sialia currucoides)	B	—
Ruby-crowned Kinglet (Regulus calendula)	—	V
Warbling Vireo (Vireo gilvus)	B	B
Orange-crowned Warbler (Vermivora celata)	—	B
Audubon's Warbler (Dendroica coronata auduboni)	B	B
MacGillivray's Warbler (Oporornis tolmiei)	—	V
Brown-headed Cowbird (Molothrus ater)	V	—
Western Tanager (Piranga ludoviciana)	V	—
Black-headed Grosbeak (Pheucticus melanocephalus)	B	B
Lazuli Bunting (Passerina amoena)	B	B
Cassin's Finch (Carpodacus cassinii)	B	—
Pine Siskin (Spinus pinus)	B	V
Green-tailed Towhee (Chlorura chlorura)	—	B
Oregon Junco (Junco hyemalis oreganus)	B	B
Chipping Sparrow (Spizella passerina)	V	—
White-crowned Sparrow (Zonotrichia leucophrys)	B	—
Summary		
Breeding:	20	14
Visitors:	17	8
Total:	37	22

* B= Breeding, V= Visitor.

TABLE 3. Avifaunal comparison of two aspen stands.

		Number of species on:				
Species	Total	area A	area B	both areas	A only	B only
All observed	45	37	22	15 (33%)	22 (49%)	8 (18%)
Breeding	25	20	14	9 (36%)	11 (44%)	5 (20%)

(Linsdale, 1938). The red-shafted flicker is a wide ranging species occurring through many types of open country or sparsely wooded regions of the valleys to the mountain forests (Bent, 1939; Bailey et.al., 1965). However, the warbling vireo, which is equally common in the valleys, in the wooded canyons, or in the mountains up to 10,000 ft, shows a decided preference for aspens and cottonwoods (Bent, 1950; Bailey et.al., 1965; Grinnell and Miller, 1944). Yellow-bellied sapsuckers nest most often in aspens (Bailey et.al., 1965) and the western wood pewee favors the dead horizontal branches of aspens as its nest site (Bent, 1942; Bailey et.al., 1965).

An analysis of the breeding bird population of area A is given in table 4. The species are grouped according to nest sites. Area A, with trees of greater average d.b.h. and height and with thicker ground cover, had 20 breeding species totalling 615 equivalent territories per 100 acres, whereas area B, the more dense stand of smaller trees and brushy undergrowth, was occupied by 14 breeding species with 267.5 equivalent territories per 100 acres. An analysis of the breeding bird population of area B is given in table 5. Nine species were found on both areas.

Preference for one habitat over another may be indicated by the difference in population densities attained by the species. When

TABLE 4. Analysis of the breeding bird population of area A.

Species categorized by nest sites	1970 Equiv. terr.	1970 ♂'s active on plot[a]	1970 Nests found	1971 Equiv. terr.	1971 ♂'s active on plot	1971 Nests found
(Ground and/or low-bush nesters)						
Lazuli Bunting	2	2	0	2	3	1
Oregon Junco	9	11	2	8.5	13	1
White-crowned Sparrow	13	13	6	12	13	1
(Cavity nesters)						
Red-shafted Flicker	5	6	5	4	5	3
Yellow-bellied Sapsucker	2.5	3	1[b]	4	5	3
Hairy Woodpecker	1	1		1	1	0
Violet-green Swallow	2	2	2	2.5	3	2
Tree Swallow	7.5	8	6	8.5	9	8
House Wren	12	13	13	13+	14[c]	13
Mountain Bluebird	4	4	4	2.5	3	2
(Canopy, branches below, or conifers)						
Broad-tailed Hummingbird	2	2	0	2	2	0
Empidonax Flycatcher	5	5	0	5	6	1
Western Wood Pewee	9	9	6	9	9	8
Olive-sided Flycatcher	1	1	0	1	1	0
American Robin	14	15	12	20	20	18
Warbling Vireo	9	9	3	10	10	3
Audubon's Warbler	5	6	0	6	6	2
Black-headed Grosbeak[d]	1	2	0	2	2	1
Cassin's Finch	6	7	1	5	6	1
Pine Siskin	5	5	0	5	5	0
Totals:	115	124	62	123	141	69
Terr. ♂'s/100 acres:		575			615	

+ Indicates less than 0.5 territories.

[a] Number of males whose territories extended onto the plot.

[b] Nest present in similar adjacent habitat.

[c] One male had two nests.

[d] Also low bush on area B

TABLE 5. Analysis of the breeding bird population of area B.

Species categorized by nest sites	1971 Equiv. terr.	1971 ♂'s active on plot[a]	1971 Nests found
(Ground and/or low-bush nesters)			
Ruffed Grouse	1	1	0
Hermit Thrush	3	3	1
Orange-crowned Warbler	4.5	6	0
Lazuli Bunting	3	3	1
Green-tailed Towhee	2+	3	0
Oregon Junco	6	6	0
Black-headed Grosbeak	2	2	1
(Cavity nesters)			
Black-capped Chickadee	1	1	1
House Wren	3.5	5	1
(Canopy, branches below, or conifers)			
Broad-tailed Hummingbird	1.5	2	0
Empidonax Flycatcher	3	3	0
American Robin	10	11	8
Warbling Vireo	9	11	0
Audubon's Warbler	4	7	0
Totals:	53.5	64	13

Territorial males/100 acres: 267.5

+ Indicates less than 0.5 territories.
[a] Number of males whose territories extended onto the plot.

the population of a species was less than ten pairs per 100 acres on both of the two areas, it was considered to show a preference, and to be characteristic of one area if its density was at least three times that of the other area. When the population density of a species was over ten pairs per 100 acres on one or both areas it was considered to show a preference if it was at least twice as abundant on one area as on the other. No definite preference for one aspen type over the other was believed to be indicated when the difference in population levels was not of the above orders of magnitude. This criterion was used to

take into account the sources of error in censusing which may have been ± 10 per cent (Martin, 1960).

Of the 25 breeding species on both areas 18 (72 per cent) showed a preference for one stand over the other. Thirteen species were characteristic of area A and five species were characteristic of area B. Seven species (28 per cent) displayed no habitat preference between the aspen types. The number of breeding species on the aspen areas and the percentage showing habitat preference are presented in fig. 2. A total of 61 per cent of the breeding pairs observed in this study showed a preference of habitat. The species showing a habitat preference for area B (36 per cent) comprised 22 per cent of the breeding pairs whereas the species characteristic of area A (65 per cent) comprised 71 per cent of the area's breeding pairs (fig. 3).

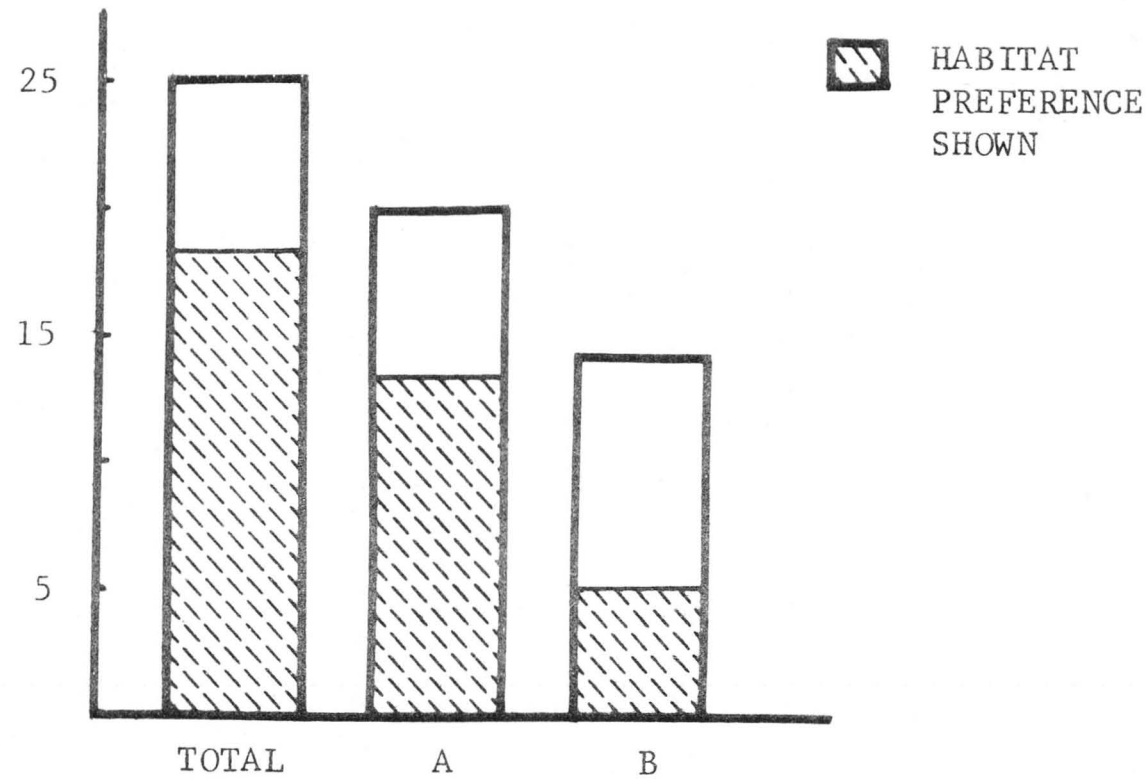


FIGURE 2. The number of breeding species on aspen areas and percentage showing habitat preference.

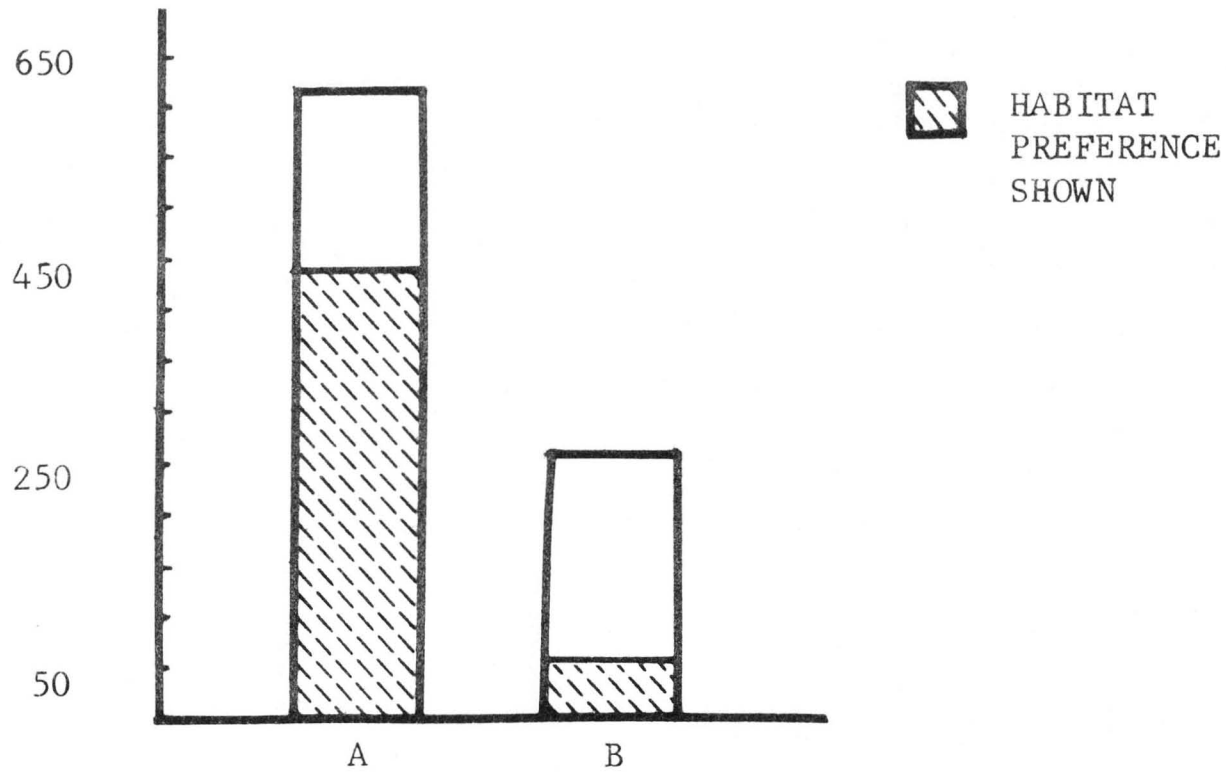


FIGURE 3. The number of breeding pairs per 100 acres in each aspen type, based on censuses of study plots described in the text, and percentage showing habitat preference.

Each of the two aspen types had a sizeable distinctive element among its breeding bird assemblage. The breeding species for the aspen areas studied are grouped by habitat preference in table 6. More cavity-nesters were found in the large trees of area A whereas more ground- and low bush-nesters were present on area B. The wide-open pattern of branch-work, preferred as lookout perches and singing posts by the western wood pewee (Grinnell et.al., 1944; Flack, 1970) was limited to area A. The high perches and open areas sought by the olive-sided flycatcher (Miller, 1942; Bent, 1942; Bailey et.al., 1965) were lacking on area B. Cassin's finches and pine siskins, which typically nest in conifers (Bent, 1968), were not found on area B which had fewer invading conifers and was farther from conifer stands.

Udvardy (1957) suggested that the denseness of a woodland is an

TABLE 6. Habitat preferences shown by breeding species.

	Species showing preference for:	
No preference shown	area A	area B
Oregon Junco	White-crowned Sparrow*	Ruffed Grouse*
Lazuli Bunting	Red-shafted Flicker*	Hermit Thrush*
Broad-tailed Hummingbird	Yellow-bellied Sapsucker*	Orange-crowned Warbler*
Empidonax Flycatcher	Hairy Woodpecker*	Green-tailed Towhee*
Warbling Vireo	Violet-green Swallow*	Black-capped Chickadee*
Audubon's Warbler	Tree Swallow*	
Black-headed Grosbeak	House Wren	
	Mountain Bluebird*	
	Western Wood Pewee*	
	Olive-sided Flycatcher*	
	American Robin	
	Cassin's Finch*	
	Pine Siskin*	

* Species found exclusively on one area.

important determinant of its bird density. Flack (1970) found that the number of bird species in aspen stands of western North America decreased with increased tree density. He also found that as the tree d.b.h. increased the number of species and the total bird density increased. Average d.b.h. increased as the tree density decreased, a trend that also was observed in the present study (refer to table 1). It is known that the diversity and/or densities of breeding birds per unit area changes in other habitats with the size of trees. The number of species comprising the coniferous forest avifauna is lower in uniform

stands of small trees (Udvardy, 1957). Comparison of an area of large maple trees with an area of small trees showed that the small maple habitat supported lower breeding bird densities per unit area (Rohwer and Woolfenden, 1969).

Breeding bird populations in forest communities vary with the fertiltiy of the forest, but are commonly between 100 and 400 pairs per 100 acres (Kendeigh, 1961). There is a wide variation of both the number of species and the densities reached by each avian species in the temperate deciduous forest of the Eastern United States. Eighty-five percent of 130 samples taken in temperate deciduous forests contained 15 to 30 avian species with a total range of 9-41 species (Udvardy, 1957). The density of breeding pairs varied from about 100 pairs per 100 acres to over 750 pairs per 100 acres. Tatschl (1967) found about 25 breeding species with over 700 breeding pairs per 100 acres for aspen stands of the Sandia Mountains in New Mexico. Twenty-six species were recorded breeding in the aspen parkland of central Canada by Bird (1930).

Hickey (1956) censused the birdlife in Itasca Park, Minnesota, in an effort to trace changes which accompanied the deciduous forest succession following the 1865 fire. Twenty brushy clearings yielded 24 species with an average of 3.0 birds per stop. Sixteen stands of young aspen (d.b.h. of three inches) yielded 27 species and an average of 3.7 birds per stop. Fifteen stops made in aspen stands of medium size (d.b.h. of four inches) yielded 26 species. The number of birds per stop increased to 6.6. In ten stops in mature aspen (d.b.h. of six or more inches) the species list remained at 26 while the number of birds per stop increased to 7.1. The aspen had reached its maximum height at

this stage and openings were frequently present.

The number of species observed by Hickey (1956) in each aspen type was about the same, however, the species composition changed by 25 per cent. The density (measured by birds per stop) of birds in the mature aspen was more than twice that for the stands of young aspen. Although the age of the trees in the present study did not differ, the average d.b.h. for the stands did show variation comparable to the Itasca Park aspen stands. The density of birds on area A (greater d.b.h.) was more than twice that of area B. The number of species observed on area A (20) was greater than on area B (14) and the species composition changed by 64 per cent (table 3).

HABITAT SELECTION

The breeding habitat of a species must provide food for the adults and young, meet the requirements imposed by structural and functional characteristics of the species, and provide shelter from enemies and adverse weather. The above can be considered ultimate factors in habitat selection as they are essential for survival and constitute the underlying reasons determining why each species breeds in its specific environment (Hildén, 1965). However, the breeding territory often is occupied long before the factors affecting the success of breeding are observable. The ground may be snow-covered and the area without available food when the birds arrive. Birds are thought to select their breeding habitat by a primarily innate reaction released by the summation of certain heterogeneous environmental stimuli, the release threshold being dependent on the internal motivation of the bird (Svärdson, 1949). Proximate factors, characteristic stimuli of the species-specific habitat, serve to release the settling reaction and

are not necessarily of direct biological significance to the species but may be of psychological importance (Lack, 1933; 1937). What these key characters are in the perception of an adequate environment is hard to determine as they are not easily tested through experiment. By observing birds in their natural habitat one can narrow down the possible cues employed and speculate as to the proximate factors involved. Height (Lack, 1933) and spacing (Miller, 1942) of the vegetation are thought to be prime factors in the choice of habitat. In the present study attributes of the terrain, foraging sites, nest sites, and location of perches were analyzed as possible proximate factors of habitat selection within aspen.

Stimuli of the terrain

Terrain refers to the physiognomic characteristics of the individual's territory proper. Probably of most importance are the surface formations and quality of the vegetational cover. The two areas studied differed greatly in surface structure, degree of slope and exposure, and in soil moisture. Area A was at the base of a north-facing slope on nearly level ground. When the breeding birds arrived in May there was still considerable snow cover which lasted in patches until the first week of June. Area B was on a SSW-facing slope which averaged 14 degrees from the horizontal. There was a 190 ft increase in elevation over the area with the upper boundary at 7,400 ft. The south exposure advanced snow melt-off by several weeks and resulted in a much drier condition during the summer. Kendeigh (1934) demonstrated that temperature, humidity, light, and wind velocity affect avian activity and behavior, and thus influence reproductive success. However, the direct effect of temperature and other climatic factors on the survival of species is hard to demon-

strate. The effect is mostly indirect through the resulting vegetation and food supply.

A vegetational comparison of the two areas is given in fig. 1. The tree trunk density was three times greater on area B than on area A. The difference in average distance between living aspen for the two plots was significant ($P < .01$), as was the difference in average d.b.h. ($P < .01$, using the 'Z'-test, Mendenhall, 1971). Although the difference in percentage canopy cover between the two areas was not significant at the .05 level (chi-square), the overstory height and structure of the canopy were different. On area A the trees reached a height of 60-70 ft and had an upper dense canopy layer with a lower sub-canopy of dead, horizontal branches and no foliage. The dividing line was about 35 ft above the ground. On area B the trees reached a height of about 35 ft with foliage starting at 15-20 ft above the ground. A sub-canopy of horizontal dead branches was not present. The shrub layer was discontinuous and of varying heights. The more centrally located and extensive chokecherry averaged 8-10 ft with a maximum of about 15 ft. The sagebrush and snowberry were continuous with the shrubs of adjacent brushland in the surrounding open areas and were about three ft in height.

The herbaceous layer on area A was continuous and lush, providing 91 per cent green ground cover. During the peak of the season the layer was five ft with some Delphinium reaching eight ft. The herbaceous layer of area B was three-four ft high with 71 per cent green ground cover. The difference between percentages of ground cover for the two areas was significant ($P < .01$ by chi-square).

The differences in tree height, density, mode of branching and

structure of tree and shrub layers between the two areas would be evident at the time of breeding bird (breeding status given in table 2) arrival since foliage and the herbaceous layer would be lacking. The ground color could provide an additional cue to future productivity as area B would be green with the start of herbaceous growth when area A was brown or snow-covered. Green could be a "negative characteristic" (Hildén, 1965) of area B to birds which would be feeding young late in the summer. The color of the ground (proximate factor), although meaningless as such, would serve as an indicator of an unfavorable breeding place (ultimate factor). Also visible with the lack of foliage would be the extent of conifer invasion. Area A averaged three subalpine fir (Abies lasiocarpa) per acre. The firs on area A were 15 ft or less in height and had invaded from the north-facing slope. Douglas-fir (Pseudotsuga menziesii) and subalpine fir present on area B exceeded the aspen canopy and averaged less than one conifer per acre.

Each avian species should be considered independently when analyzing its dependency on the environment, as each species may have a different set of limiting factors (Kendeigh, 1945).

Nest sites

Seven species (54 per cent) showing preference for area A were cavity nesters. Three of these, the red-shafted flicker, yellow-bellied sapsucker, and the hairy woodpecker were capable of excavating their own cavities whereas the two swallows, house wren, and mountain bluebird were dependent on other birds for their cavities. The mean heights of the cavities used during 1970 and 1971 are presented in table 7 and fig. 4. Comparisons of measurements for all the species showed no

TABLE 7. Mean heights of cavities for species characteristic of area A.

	No. of cavities measured		Mean height (in ft)	Range (in ft)	S.D.
	1970	1971			
House Wren	13	13	9.4	1.5-25	6.09
Violet-green Swallow	2	2	11.3	9.0-15	2.87
Tree Swallow	7	8	12.2	6.0-20	3.28
Mountain Bluebird	4	2	12.7	8.0-16	3.21
Red-shafted Flicker	5	3	13.0	8.0-20	4.23
Yellow-bellied Sapsucker	2*	3	17.2	12.0-25	7.12

* One excavation not used as nest, 1970.

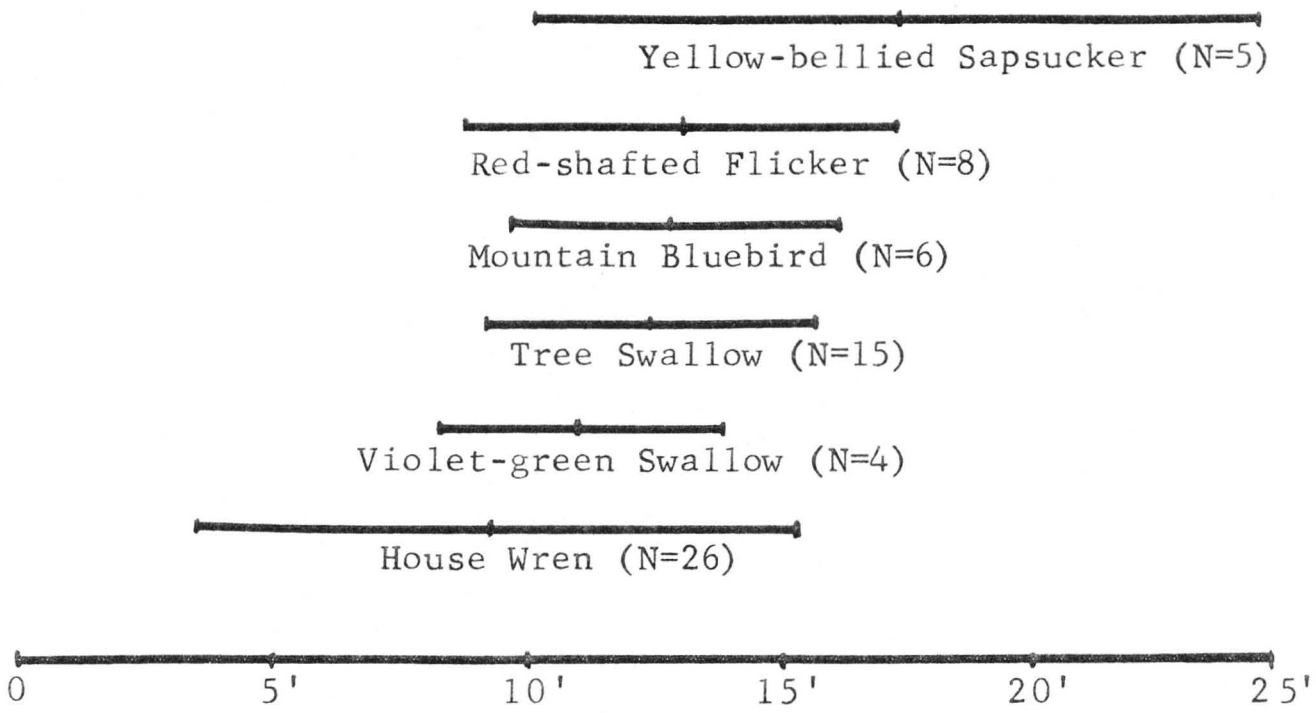


FIGURE 4. Distribution of cavities in relation to height of cavity above ground. The mean height and standard deviation are given for each species.

significant difference in heights of cavities used (using Student's 't' test). It appeared that the cavity nesters were not selecting holes at a particular height above the ground, since the same cavity, without observable alteration, sometimes was used by a different species in the successive year. The combinations of species using the same nest hole in 1970 and 1971 are shown in table 8. Twenty-one cavities known

TABLE 8. Number of times combinations of species used the same cavity.

1970 \ 1971	Red-shafted Flicker	Yellow-bellied Sapsucker	Tree Swallow	House Wren	Mountain Bluebird	Violet-green Swallow
Red-shafted Flicker	1	·	1[a]	·	·	·
Yellow-bellied Sapsucker	·	1	·	1[b]	·	·
Tree Swallow	1	·	1	·	·	·
House Wren	·	·	·	2	·	·
Mountain Bluebird	·	·	·	1	·	1
Violet-green Swallow	·	·	·	·	·	1

[a] Tree Swallow cavity lost to House Wren during 1971 season.

[b] Yellow-bellied Sapsucker excavation not used as nest in 1970.

to have been used in 1970 remained vacant in 1971. The area also contained numerous other cavities which appeared to be suitable as nest holes. Unless subtle factors made many holes unsuitable, the area contained numerous surplus cavities. The observation of interspecific conflicts (usually involving house wrens) in the vicinity of nest holes does not invalidate the conclusion that cavities were in excess of demand. In only one observed case were house wrens successful in displacing a pair of tree swallows, and then the swallows found an alternative hole close by. Thus the availability of nest-holes did not appear to be a limiting factor in area A.

No woodpeckers were present in area B since cavity excavation is limited to trees of sufficient d.b.h. Flack (1970) offered the generalazation that the number of woodpeckers increased in aspen when the average d.b.h. was above six inches and there were between 100 and 300 trees per acre. The average d.b.h. of trees in area B was 4.74 inches and there were 349 aspen per acre. Bird (1930) found the flicker restricted to the neighborhood of mature trees which formed its nesting sites. All species are known to be dependent upon the availability of their specific nest sites. Lack of available nesting cavities acted as an ecological minimum factor in area B. Flack (1970) showed a correlation between the number of species or individual birds dependent upon cavities and the number of species of birds which excavate cavities in aspen.

The ruffed grouse, hermit thrush, orange-crowned warbler and green-tailed towhee showed a habitat preference for area B. The above are all known to be low bush-nesters or ground-nesters in shrubby areas. The black-capped chickadee, also showing preference for area B, nested in a

knot-hole which it had enlarged in a small aspen.

Foraging

The method and location of feeding were observed rather than food type because it is believed that motor patterns are basic to feeding behavior, and that the particular type of food acquired is the result of such behavior (Crowell, 1962). The distinction between feeding directed toward animal or vegetable food was usually impossible to make in the field. Classifications of feeding methods used were: ground (feeding on the ground), bark (feeding on woody parts of vegetation), foliage (feeding in leafy parts of trees), hover (taking insects or nectar from vegetation while in flight), and hawking (taking flying insects while in flight).

The observed distributions of feeding methods in area A are presented in fig. 5. The shaded areas on the graph represent the

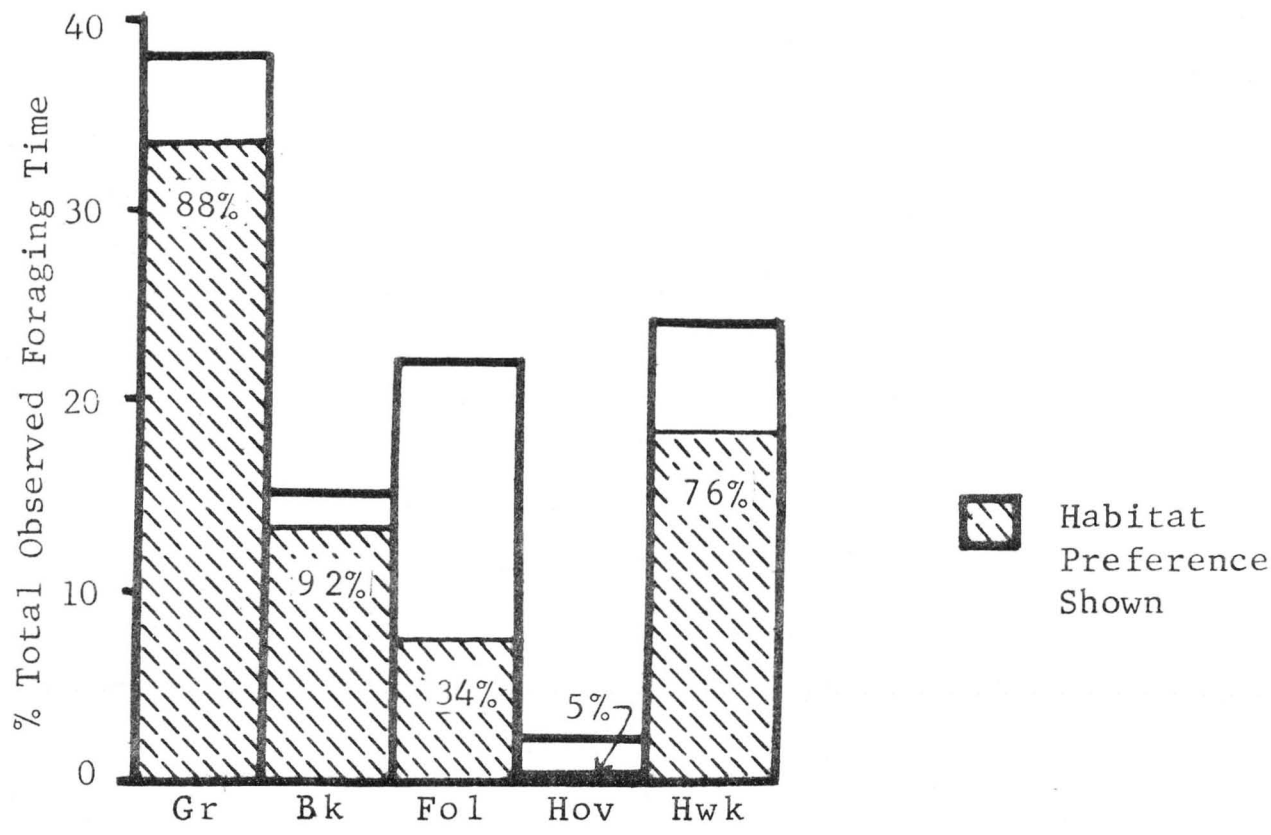


FIGURE 5. The observed distributions of feeding methods in area A, 1971, and percentage by birds showing a habitat preference for area A. Gr = Ground, Bk = Bark, Fol = Foliage, Hov = Hover, Hwk = Hawking.

percentage of each method demonstrated by birds showing a habitat preference for area A. Observations were made on all species breeding on area A (table 2) except for the lazuli bunting which made up 1.6 per cent of the total population and did not show a preference. The feeding methods of (1) the total pairs of birds showing a habitat preference for area A, and (2) the population of birds present on area A which did not show a habitat preference, are compared in fig. 5. A high percentage of the ground and bark feeding and hawking was done by the preference-showing birds. Characteristics of the ground cover, bark, and conditions for hawking (open sub-canopy, height to bottom of canopy and canopy height) differ considerably between areas A and B. A greater percentage of the foliage- and hover-feeding was done by the birds showing no habitat preference. The aspen foliage was not appreciably different between the two areas except in height above the ground. On both areas the majority of hovering was done by the broad-tailed hummingbird while feeding on the nectar of horse mint (Agastache urticifolia).

The feeding methods used by each species of the population showing a habitat preference for area A are presented in fig. 6. Trunk feeding was predominant among two cavity excavating species- yellow-bellied sapsucker and hairy woodpecker. The red-shafted flicker foraged on the ground. According to Grinnell, Dixon, and Linsdale (1930) Cassin's finches may forage in aspens but a greater share of their foraging is done on the ground in clearings. In 1971 all observed foraging for the Cassin's finch occurred on bark and foliage while in 1970 foraging was done extensively on the ground (not included in fig. 6). Cassin's finches appear to be opportunistic feeders. Hawking was the only

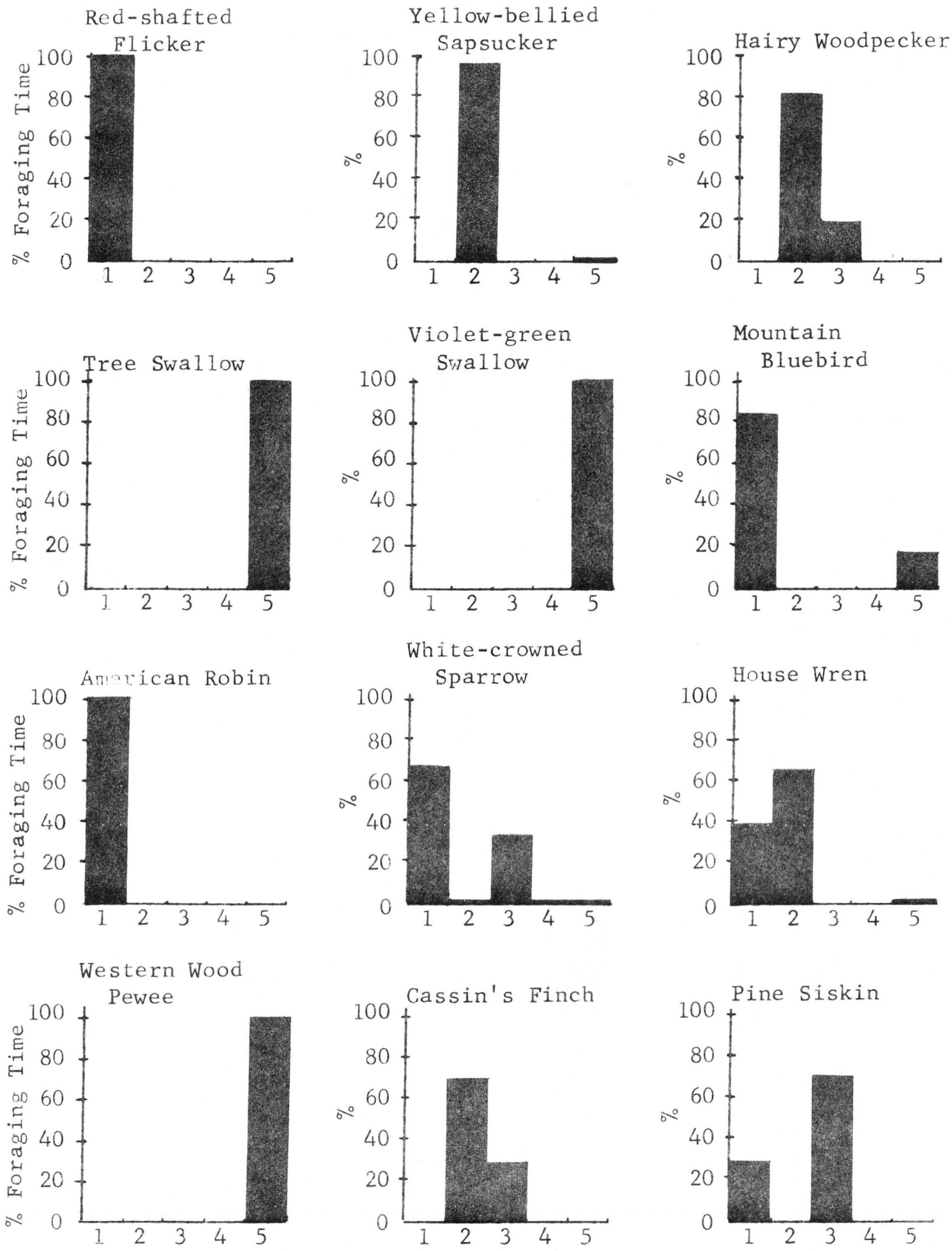


FIGURE 6. Distribution of feeding methods on area A in 1971 for individual species showing a habitat preference. (1) Ground, (2) Bark, (3) Foliage, (4) Hover, (5) Hawking.

observed foraging method used by the swallows on area A in 1971. However, Bent (1942) reports that the tree swallow eats berries or seeds as well as insects while the violet-green swallow lives entirely on insects taken on the wing.

The feeding methods for each of the individual species showing no habitat preference between areas A and B are given in fig. 7. For foraging, non-preference birds utilized structures which differed little between the two aspen types. The warbling vireo and black-headed grosbeak were exclusive foliage feeders- both foraged by hanging upside down on the tips of the vegetation. The broad-tailed hummingbird fed

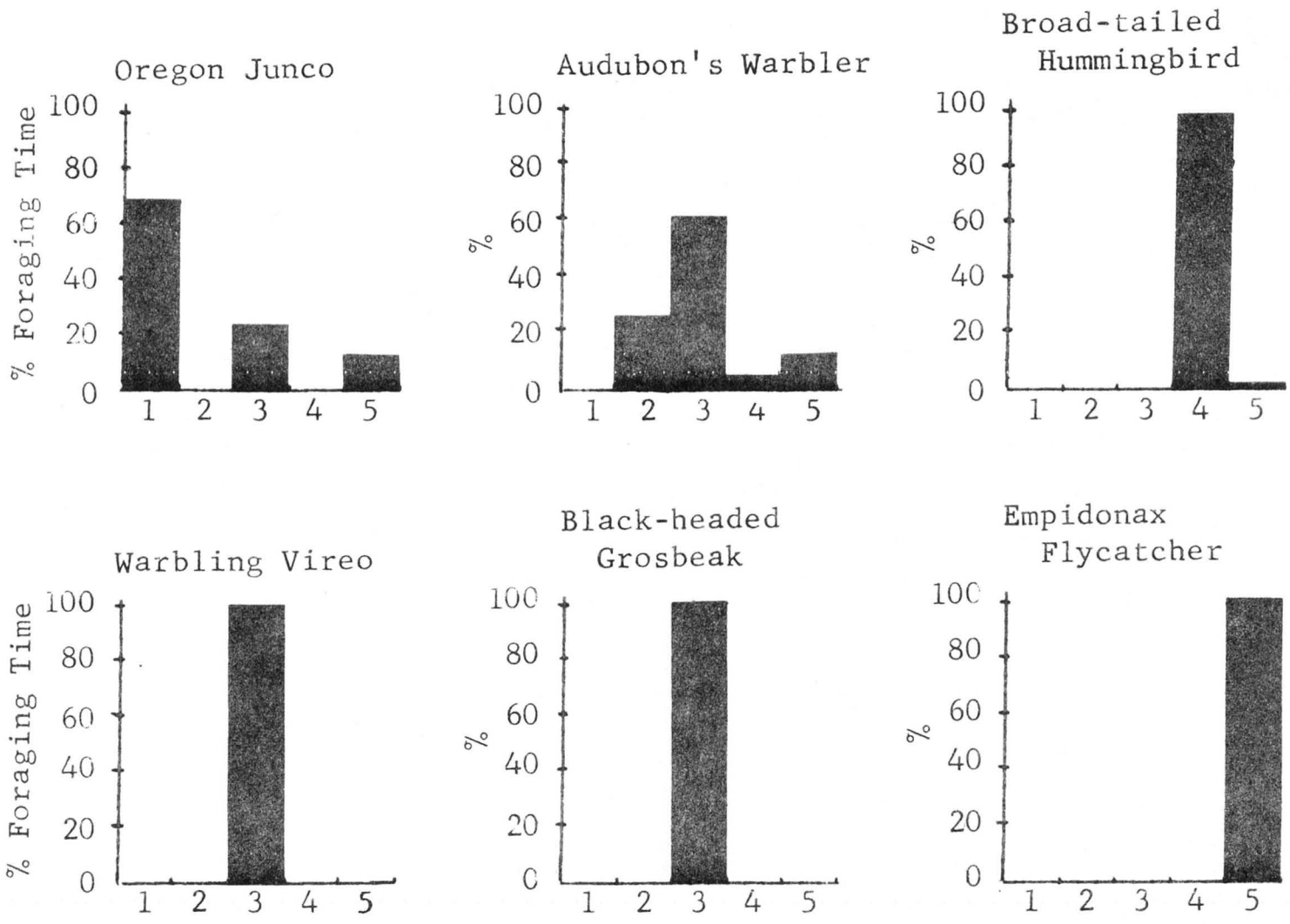


FIGURE 7. Distribution of feeding methods on area A in 1971 for individual species showing no habitat preference between aspen types. (1) Ground, (2) Bark, (3) Foliage, (4) Hover, (5) Hawking.

on the nectar of flowering plants such as Agastache and Senecio which occurred on both areas. The Empidonax flycatcher foraged by hawking low in the aspens while the foraging activities of the Oregon junco and Audubon's warbler were spread over several methods and included foliage feeding.

The observed distribution of foraging heights for all species on area A (except the lazuli bunting) is given in fig. 8. The shaded area gives the percentage at each stratum demonstrated by species showing a habitat preference for area A. Seventy-eight per cent of all foraging above 30 ft and 86 per cent of the ground-level foraging were accomplished by species characteristic of area A. The 0-½ ft stratum included low vegetation such as that utilized by the broad-tailed hummingbird early in the season. The differences in per cent ground cover and canopy heights between area A and area B were significant.

The American robin and red-shafted flicker, both ground-feeders (fig. 6), spent 100 per cent of their observed foraging time in the

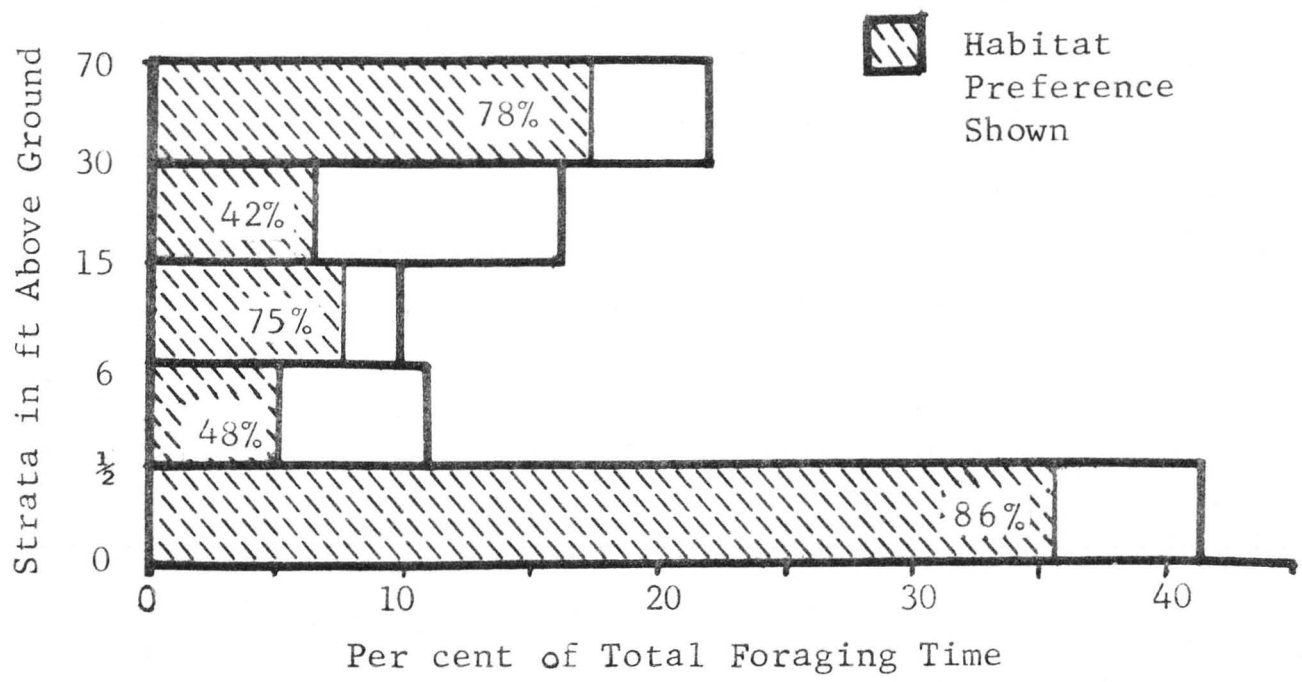


FIGURE 8. Observed distribution of foraging heights in area A and the percentage at each level by birds showing a habitat preference for area A, 1971.

0-½ ft stratum. Cassin's finches were observed foraging above 30 ft 100 per cent of the time, however, they would also occupy the 0-½ ft stratum in years when they foraged on the ground. Tree swallows and violet-green swallows were observed hawking above 30 ft 100 per cent of the time. The distributions of foraging heights for other species showing a habitat preference for area A are presented in fig. 9. The yellow-bellied sapsucker and hairy woodpecker were predominantly bark feeders. Foraging activities for the yellow-bellied sapsucker were distributed among all strata except 0-½ ft. This indicates that neither trees of a particular height nor particular heights on the trees were selected. The foraging activities of the hairy woodpecker included the 0-½ ft stratum which contained stumps and fallen trees.

All of the species showing no habitat preference between area A and area B spent 50-100 per cent of their foraging time below 30 ft (fig. 9). The warbling vireo and the black-headed grosbeak both foraged exclusively in the foliage. The black-headed grosbeak spent over 50 per cent of its time below 15 ft whereas the warbling vireo foraged entirely above 15 ft.

The Empidonax flycatcher and western wood pewee did all their observed foraging by hawking. A comparison of the distributions of foraging heights used by the two species is given in fig. 10. All the Empidonax flycatcher's foraging was done below 30 ft with 82 per cent between ½ and 6 ft, whereas the pewee's foraging was more evenly distributed between the ½-6 ft and 10-15 ft strata with 37 per cent above 30 ft. The foraging and singing radius of the olive-sided flycatcher comprised the upper airways and exposed tree tops well above 30 ft.

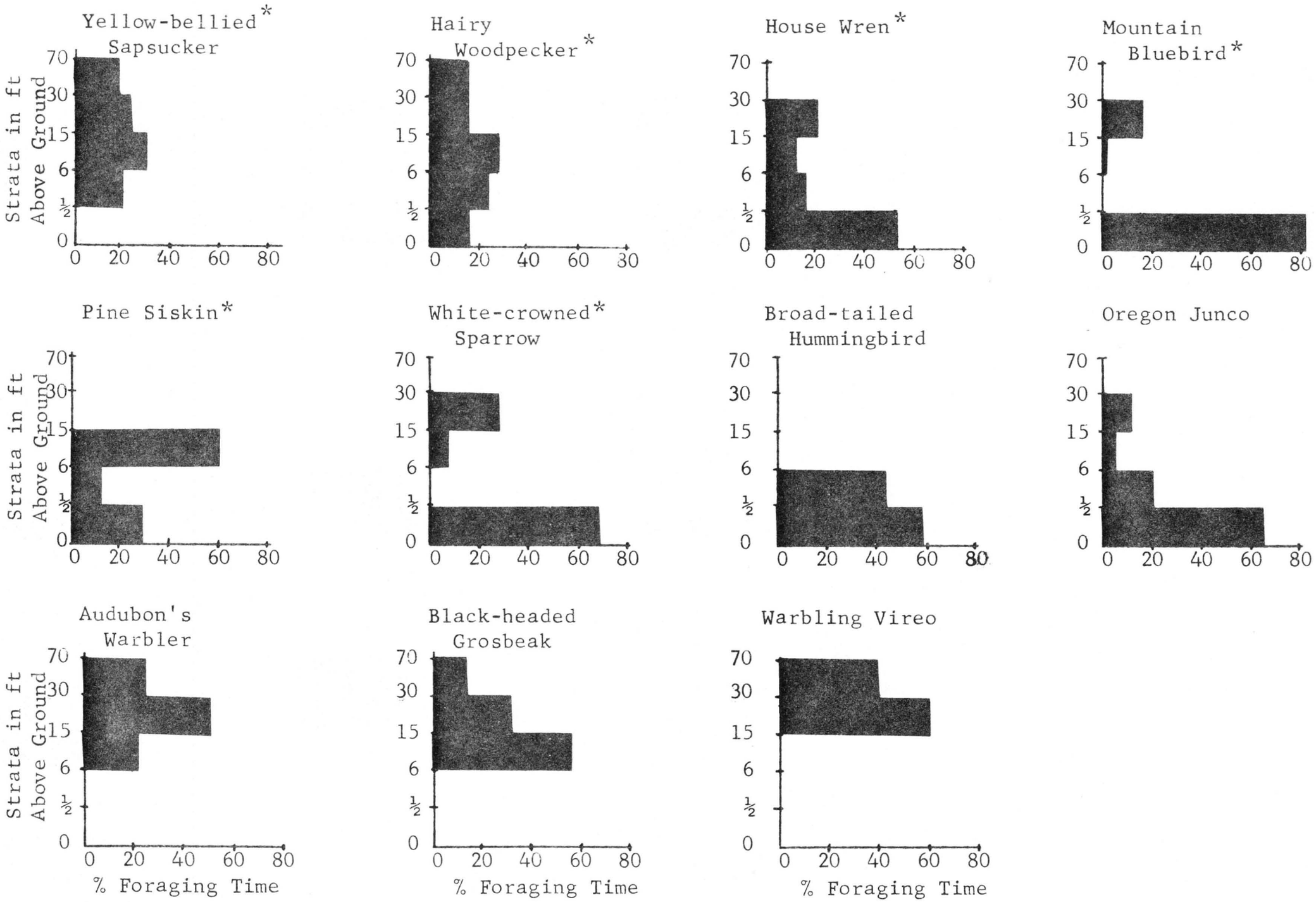


FIGURE 9. Distribution of foraging heights for some of the individual species on area A in 1971.
* Species showing a habitat preference for area A.

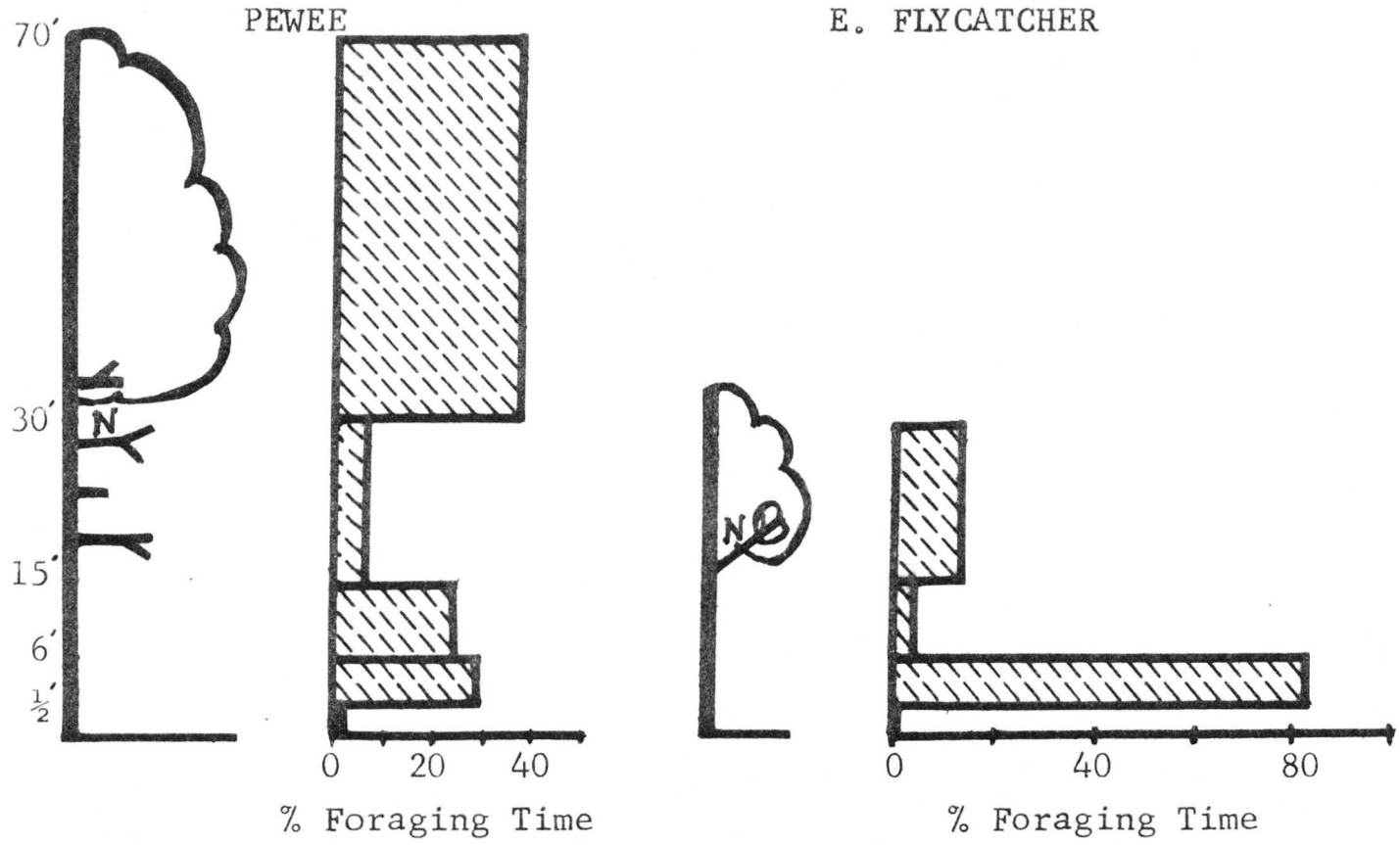


FIGURE 10. Comparison of foraging heights and nest sites (N) used by the western wood pewee and the Empidonax flycatcher on area A, 1971.

On area A the number of individual flycatchers was five times as great as on area B. Flack (1970) found that the number of birds feeding by flycatching increased with increased average height to the bottom of the canopy. The bottom of the canopy averaged 20 ft higher for area A than area B. Flycatching was also an important method of feeding for the mountain bluebird after the ground vegetation had grown above a few feet. However, the pairs flew into more open areas outside plot A to forage; thus the percentage shown in fig. 6 is lower than actually occurred. Mountain bluebirds were not found on area B.

Species showing a habitat preference for area A utilized structures which were characteristic of area A. The lush ground cover, the bark of the trees of large d.b.h., the open sub-canopy of dead branches and the high canopy on area A were used in foraging by the preference

showing birds. Species showing no habitat preference between area A and area B foraged in the foliage at heights not limited to area A (below 30 ft) or hovered in the flowering understory vegetation common to both areas.

Perches

The type and quantity of available perches may have a marked effect on the ecological distribution of certain birds (Emlen, 1956). To assess the use of various structures in the environment as perches for foraging, singing, nesting or loafing, timed observations were made of all activities for 16 of the breeding species in area A. A summary of the percentages of total time spent in different zones for each species is given in table 9. The dead branch element showed a higher percentage of use by those birds exhibiting a habitat preference for area A than by species showing no habitat preference, e.g. the western wood pewee used dead branches for perches 90 per cent of the time compared to 33 per cent for the Empidonax flycatcher. Horizontal, heavy branch stubs were the nest sites for pewees (fig. 10) whereas the Empidonax flycatcher nested in aspen saplings, its major perch (57 per cent). Activities of the tree swallow, including copulation and care for fledglings, were all observed to occur on the dead branches. Swallows foraged while continuously on the wing.

Nest, foraging, and perch requirements can be determined by observing a species within its natural habitat. By comparing the structural characteristics of a species' habitat with a similar habitat for which the species does not show preference, limiting factors may be indicated. Similarly, through comparison of the structures of two habitats between which a species does not show a preference, one can

TABLE 9. Percentage of observed time spent within various zones in area A.

Species	Total Observed Time (sec)	Per Cent Of Total Observed Time									
		Ground	Main Trunk	Dead Branch	Upper Branches	Foliage	Stump	Dead Tree	Fallen Tree	Conifer	Sapling
Oregon Junco*	1889	49	0	14	0	0	0	0	8	10	26
White-crowned Sparrow	2496	34	0	28	0	11	3	0	0	22	0
Red-shafted Flicker	923	26	8	54	0	0	13	0	0	0	0
Yellow-bellied Sapsucker	2428	0	38	13	16	0	0	2	2	28	0
Hairy Woodpecker	1347	0	9	34	0	15	19	0	24	0	0
Tree Swallow	2102	0	0	100	0	0	0	0	0	0	0
House Wren	2586	14	3	38	2	0	3	3	38	0	0
Mountain Bluebird	2845	13	0	68	0	0	0	0	0	0	0
Empidonax Flycatcher	1394	1	0	33	3	0	0	0	0	3	57
Western Wood Pewee	2765	0	0	90	0	0	4	3	3	0	0
American Robin*	2621	60	0	38	0	0	0	0	0	0	0
Warbling Vireo*	586	0	0	18	0	56	0	25	0	0	0
Audubon's Warbler*	714	0	0	31	36	16	0	5	0	15	0
Black-headed Grosbeak*	593	0	0	0	12	88	0	0	0	0	0
Cassin's Finch	1097	0	0	64	36	0	0	0	0	0	0
Pine Siskin	545	10	0	57	18	0	3	0	0	12	0

* Species showing no habitat preference between areas A and B.

determine the range of vegetational components meeting the nesting and foraging requirements of the species.

In this study two aspen habitats were analyzed with respect to structure. The nesting and foraging requirements were observed for those birds indicating (1) a habitat preference for area A, (2) a preference for area B, and (3) no habitat preference between areas A and B. If the structural characteristics visible at the time of bird arrival and the habitat requirements of given species are known, one can speculate as to the proximate factors functioning in the release of the settling reaction.

Site tenacity may have been influential in the return of individuals which previously had nested on the areas. The tree height, tree spacing, available cavities, presence of horizontal, heavy branch stubs, and invading conifers as well as the presence of returnees were available cues for birds which had not nested previously on area A. Birds characteristic of area B had the cues of tree height and the two-layered vegetational structure of dense trees and shrubs. Nesting activities were initiated and completed earlier on area B (south-facing) than on area A (north-facing). Depending on individual internal motivation, birds of species showing no habitat preference between the aspen types may have been influenced in their settling on area B first by the exposure of the areas, and the condition of developing herbaceous undergrowth.

Stimuli involved in the releasing mechanism of the settling reaction, such as nest-sites, foraging-sites, and perches, may be directly important in the life of the birds. The ultimate and proximate factors of habitat selection may thus coincide.

SUMMARY

The breeding avifaunas of two types of aspen stands in northern Cache County, Utah, were censused using 20 acre grids. Of 25 regularly breeding species, 18 showed a preference for one stand over the other. Thirteen species were characteristic of tall, well spaced trees with a sub-canopy of horizontal dead branches and thick ground cover. Five species occurred only in the dense stand of small trees with a discontinuous shrub layer. The breeding bird assemblage in the large trees was more diverse (20 species) than in the small trees (14 species). The large trees also supported more breeding pairs per 100 acres (615 vs. 267.5).

The requirements of the bird species present closely paralleled the nature of the vegetation in the two areas. More cavity-nesters were found in the trees of greater d.b.h., whereas more ground- and low bush-nesters were present in the small trees. The horizontal, heavy branch stubs preferred by pewees and tree swallows and the high perches and open areas sought by the olive-sided flycatcher were limited to the stand of large, well spaced trees. Cassin's finches and pine siskins were not found in the stand of small trees which had fewer invading conifers and was farther from conifer stands.

The distribution of feeding methods used by the bird population showing a habitat preference for the large tree area was compared with that for the bird population also present in the large trees but not demonstrating a habitat preference. A high percentage of the ground- and bark-feeding and hawking was done by the preference-showing birds whereas more foliage- and hover-feeding was done by the species overlapping both habitat types. Characteristics of the ground cover,

bark, and conditions for hawking (open sub-canopy, height to bottom of canopy, and canopy depth) differed considerably between the two aspen stands while the aspen foliage did not differ appreciably. The majority of hovering on both areas was done by the broad-tailed hummingbird while feeding on the nectar of understory flowering plants. Comparison of foraging heights showed that high percentages of the foraging done at above 30 ft and at the ground-level were accomplished by species characteristic of the tall trees. All of the species not displaying a habitat preference spent 50-100% of their foraging time below 30 ft.

By comparing the structural characteristics of the two aspen types, limiting factors were indicated for species occurring in only one of the two areas. Similarly, the range of vegetational components meeting the nest, foraging, and perch requirements was shown for species not demonstrating a habitat preference between the aspen types.

The differences between the two areas in tree height, tree density, mode of branching, available cavities, structure of tree and shrub layers, and extent of conifer invasion were evident at the time of breeding bird arrival. The above, as well as the presence of returnees, are thought to be proximate factors functioning in the release of the settling reaction in birds which had not nested previously in the area.

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