TEMPORAL CHANGE AND HABITAT PREFERENCE OF SOME MONTANE BREEDING BIRDS

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Birds are highly visible animals in terrestrial communities, and changes in species composition and numbers with time can illustrate community dynamics (Lack 1966, MacArthur 1971). This five-year quantitative study was conducted to determine the patterns of change or balance that occurred throughout a typical avian reproductive season in a montane community of Colorado's Front Range.

Factors governing bird presence and density have been discussed by Lack (1954, 1966, 1968), Immelman (1971), MacArthur (1971), and many others. In this study I was able to test the following hypotheses: (1) most breeding species show constant yearly densities; (2) most species show changes in relative density within the yearly cycle; (3) breeding times of the different species are well spread throughout the spring and summer season; (4) bird species show strong vegetational preferences; and (5) edge effect and patchiness of vegetation are of minor importance in determining relative avian density.

STUDY AREA AND METHODS

A 20 hectare tract in Crow Gulch on the lower slopes of Pikes Peak, near Colorado Springs, Colorado, was censused for five breeding seasons, 1967 to 1971. The area was diagonally bisected by a small stream, and the slopes on each side of the stream supported different types of vegetation. The northern, south-facing slope was covered with Ponderosa Pine (*Pinus ponderosa*), and the southern, north-facing slope with Douglas Fir (*Pseudotsuga menziesii*). Stands of aspen (*Populus tremuloides*) and Spruce (*Picea* spp.) were found along the stream. Access to the area was restricted, and the study site was relatively undisturbed. Elevation ranges from 2683 to 2757 m, and map coordinates are 38°55′N × 105°W.

A grid system of 218 quadrats, each approximately 0.1 ha was surveyed with compass and steel tape. The intersections of survey lines were marked with high-visibility paint for quick identification of location. Quadrats were censused using the Williams spot-mapping method (Williams 1936, see also Kendeigh 1944) which involves determining the distribution and numbers of birds on a grid. To census, I walked unhurriedly along the alternate grid lines between 06:00 and 11:00. Early evening surveys proved less fruitful. As bird presence and flight direction were noted, it usually was apparent if the same bird was observed twice. For all birds seen or heard, species, number, sex, location, and activity were recorded. A minimum of 12 morning surveys were made each year from early March until August, though most frequently during June and July, for a total of 270 field hours in 68 tours.

The numbers of individuals of each species seen per census do not give actual densities, for not all birds are seen in any one census. Enemar (1962) estimated even half to one-third of the singing males are missed by a lone observer. Spot-mapping a species repeatedly during the breeding season does allow density of breeding pairs to be estimated accurately (Kendeigh 1944) because territoriality is depicted. However, in this study the numbers seen per census can be used as an index of relative density because the study area was covered consistently in a systematic fashion. Even though some birds were not seen, the visibility of the various species remained fairly constant.

In 1967 each quadrat was inspected for predominant vegetation and assigned to one of six major vegetation types. Inspections were repeated each year to test correctness of assignment. The vegetation was also sampled by quadrat and transect methods for quantitative description. In 1972, I measured the change in foliage densities as the vegetation grew from spring to fall. All vegetation measurements showed stable stands of both mature and young individuals.

The Douglas Fir and Ponderosa Pine usually grew in pure stands except in edge areas or near ridgetops. Where there were clinal gradations from one vegetation form to another, the quadrat was so split. A small amount of Limber Pine (*Pinus flexilis*) was considered a normal component of the more dominant Ponderosa Pine. In Mixed Forest areas, mature trees of more than two species were present in numbers. These usually were located in edge situations on north-facing slopes or in areas of topographic extreme. In the Spruce-Aspen area the stream bottom was wide, and bogs and seeps were found. In the Willow (*Salix*)-Aspen vegetation the willows lined a clear running creek, and aspens occurred in the shade, extending into dry gullies on the north-facing slope. Open Meadow, the sixth vegetation type, often was bordered by Willow-Aspen.

Climatic data, vegetation, and bird information were compiled by year and then combined to produce the tabular results of the following section.

RESULTS

AVIAN DENSITIES

Species and numbers of birds seen each year are shown in table 1; the birds are denoted as visitors, breeding pairs, or lone singing individuals. The latter, always male when sex was determined, had no visible mates and showed no breeding activity except vocalization. They may have been surplus males, juvenile non-breeders, or actual breeders. Because so many surveys are based on the presence of singing males only (e.g., Enemar

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TABLE 1. Bird densities, Crow Gulch, Colorado, 1967–1971.

Species	Birds in 20 ha study area[a]					x̄ No. brdg prs/40 ha
	1967	1968	1969	1970	1971	
Cathartes aura			V			
Accipiter cooperii	1 pr			1 b	1 b	0.8
Buteo jamaicensis	V		V	V	V	
Buteo spp.			V			
Dendragapus obscurus		1 pr	1 b	1 pr		1.0
Columba fasciata				V		
Zenaida macroura	V	V	V	V	V	
Bubo virginianus	V	V		V		
Chaetura pelagica		V				
Selasphorus platycercus	2 pr	3 pr	2 pr	1½ pr	3 pr	4.6
S. rufus	V					
Colaptes auratus	2 pr	2 pr	2 pr	2 pr	1 b	3.4
Sphyrapicus varius			V			
S. thyroideus	1 pr	2 pr	1 pr	1 pr	1 pr	2.4
Dendrocopos villosus	1 pr	1 pr	1 pr		1 pr	1.6
D. pubescens	1 pr					0.4
Empidonax difficilis	1 b	1 b		1½ pr	1 b	1.2
Contopus sordidulus		1 b	1 b	1 pr	1 b	1.0
Tachycineta thalassina	1 pr	2 pr	1 b	V	V	1.4
Cyanocitta stelleri	2+ pr	3–4 pr	2 pr	3½ pr	3½ pr	5.8
Pica pica					V	
Corvus corax	V		V	V		
C. brachyrhynchos		V		V	V	
Nucifraga columbiana	V	V	V	V	V	
Parus atricapillus		V	V			
P. gambeli	6 pr	6 pr	6 pr	5½ pr	6 pr	11.8
Sitta carolinensis		½ pr		½ pr	V	0.4
S. canadensis			1 b	2 pr	1 b	1.2
S. pygmaea	2½ pr	3+ pr	4 pr	2½ pr	3 pr	6.0
Certhia familiaris			1 b	1 b	1 pr	0.8
Troglodytes aedon	3½ pr	3 pr	4½ pr	4 pr	4 pr	7.6
Turdus migratorius	2 pr	2+ pr	3½ pr	3½ pr	2½ pr	5.4
Catharus guttatus		V		V		
Sialia mexicana		1 pr	V	V	1 b	0.6
Myadestes townsendi	1 b	1 pr	3 pr	3 pr	3½ pr	4.4
Regulus calendula		1 pr	1 pr		2 pr	1.6
Vireo gilvus	1 b	1 pr	2 pr	2 pr	3 pr	3.4
Vermivora virginiae	V			V	V	
Dendroica coronata auduboni	1 b	1 b	1½ pr	1½ pr	2½ pr	2.8
Oporornis tolmiei	1–2 pr	2 pr	1 pr	2 pr	1 pr	3.0
Piranga ludoviciana		1 pr	V	V	1 b	0.6
Pheucticus melanocephalus			V	V		
Spinus pinus		V	V	V	V	
Loxia curvirostra				V		
Chlorura chlorura	1 pr	2 pr	1½ pr	1½ pr	1½ pr	3.0
Pipilo erythrophthalmus				V		
Junco h. hyemalis				V		
J. h. oreganus		V	V		V	
J. caniceps	6 pr	6 pr	6 pr	6 pr	6 pr	12.0
Melospiza lincolnii			1 b	1 b		0.4
Total no. species	26	32	35	39	33	
Brdg. species	19	23	22	22	23	
Visitor species	7	9	13	17	10	
Total brdg. prs	37	47	48	48.5	51.5	
Brdg. prs/40 ha	74	94	96	97	103	
x̄ No. brdg. prs/40 ha						93.0

[a] V = visitor species; pr = breeding pair; ½ pr = breeding pair with half of territory within study area; + = breeding pair with less than half of territory within study area; b = lone, singing bird.

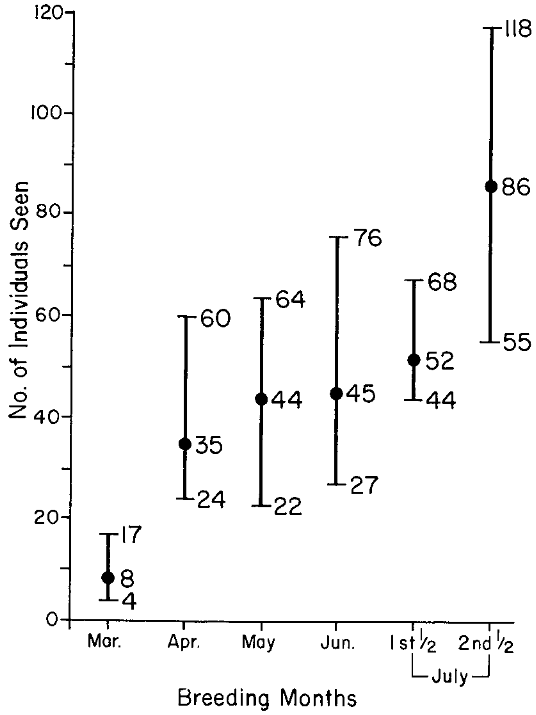

FIGURE 1. Changes in density of all species within the year, based on data from 1968 to 1971. Black dots = means, vertical lines = ranges.

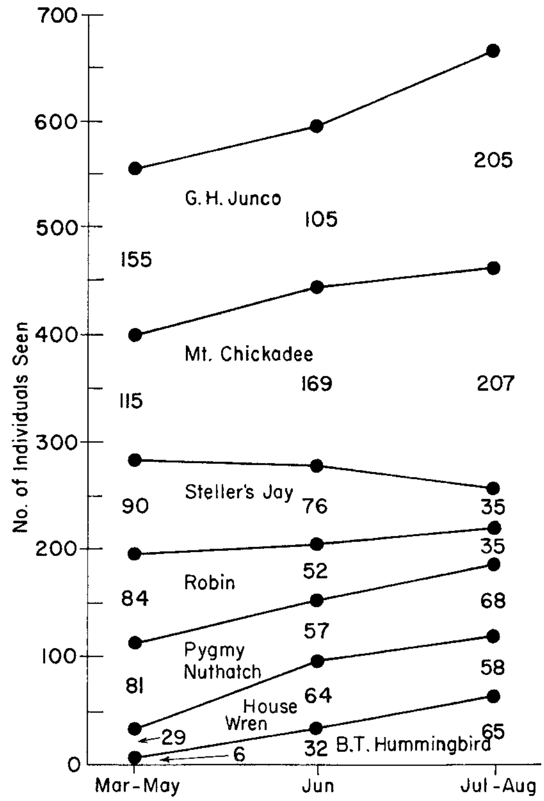

FIGURE 2. Relative density changes of the seven dominant species within the year. Numbers on vertical axis show cumulative number for all species depicted, and numbers within figure by each black dot show the species average number at that time of year.

1959, 1962, Vindokurov 1963, Balda 1969), these birds were included as breeding pairs in the totals. Visitor species include large raptors and corvids whose home ranges included the study area, altitudinal migrants during spring and fall, and winter residents which bred elsewhere.

Fifty species bred on or visited the study area, but on the average, only 78% of these were seen in any one year. In 1970, when most species were seen, the number of breeding species showed no real increase but the number of visitors did. The number of breeding species was reasonably constant from year to year though the species sometimes varied. The most numerous species were the Mountain Chickadee (*Parus gambeli*) and the Gray-headed Junco (*Junco caniceps*). These two represented less than 10% of the species present in any one year but contributed about 25% of the breeding pairs. The seven most common species, including the House Wren (*Troglodytes aedon*), Pygmy Nuthatch (*Sitta pygmaea*), Robin (*Turdus migratorius*), Steller's Jay (*Cyanocitta stelleri*), and Broad-tailed Hummingbird (*Selasphorus platycercus*), accounted for one-third of all species present but constituted over 50% of all breeding pairs and showed constancy in numbers during the years of the study (table 1).

Though most species remained constant, the numbers of Townsend's Solitaire (*Myadestes townsendi*), Warbling Vireo (*Vireo gilvus*), and Yellow-rumped Warbler (*Dendroica coronata auduboni*) increased during the five year period. None of these changes was significant ($0.25 > P > .10$, Chi-square Test, 4 d.f.). The numbers of Violet-green Swallow (*Tachycineta thalassina*) and Common Flicker (*Colaptes auratus*) decreased, but not significantly ($0.15 > P > 0.06$, Chi-square Test, 4 d.f.).

The overall increase in total pairs, from 37 in 1967 to 51.5 in 1971, was not a function of more census time or better coverage but may have resulted from greater knowledge of the area. The increase in numbers of solitaires, vireos, and warblers accounted for only half of the difference; the other half was well distributed among the remaining species.

AVIAN DENSITY

There is a definite seasonal increase (fig. 1) in the number of birds sighted per census ($\chi^2 = 48.01$, $P < 0.01$, 4 d.f.; July treated as

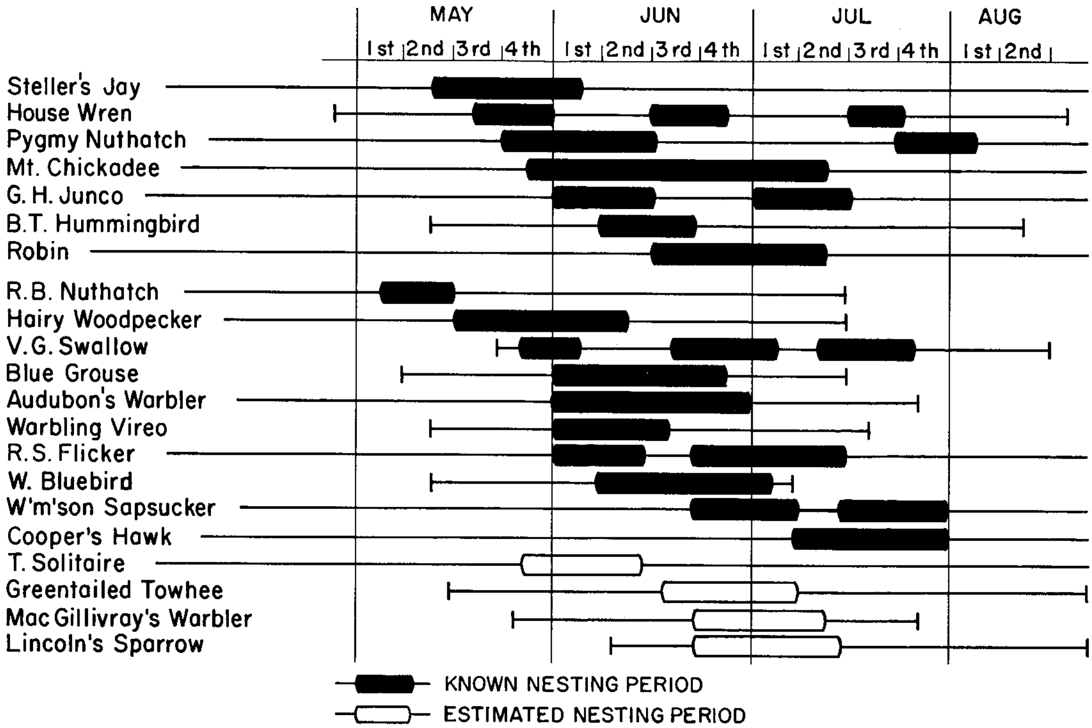

FIGURE 3. Temporal spacing of breeding. The length of the horizontal line indicates the duration of the species presence in the area.

one month, $\bar{x} = 69$; tested using the average number of birds sighted per census during each month for the last four years of the study). Of the seven dominant species, the Broad-tailed Hummingbird, House Wren, Mountain Chickadee, and Gray-headed Junco all showed this same seasonal increase (numbers for each species listed in fig. 2), and the total number for all species increased from 550 to 660. However, the numbers of Robin, Steller's Jay, and Pygmy Nuthatch decreased (numbers in fig. 2). The high numbers of these latter species in early spring censuses may have been due to altitudinal migrants passing through the study area. This also is shown in the high April count (fig. 1). The low July and August numbers of these species may have resulted from post-breeding dispersal of young and/or adults to other elevations. The high numbers of July birds (fig. 1) were due to large flocks of juvenile juncos and chickadees.

TEMPORAL SPACING OF BREEDING ACTIVITY

Figure 3 shows the temporal spacing of nesting activity of the different species. Three separate nesting periods are depicted for three species. This does not mean that any one pair had three consecutive nests but merely that nests of that species were seen at those times. The absence of the shaded area means that nests were not found in that time period. For those species whose nests were not found, nesting periods were estimated on the basis of timing of male vocalizations. In several species, such as the Ruby-crowned Kinglet (*Regulus calendula*), birds sang continuously during their stay in the area, and in others, such as the Brown Creeper (*Certhia familiaris*) and the Western Wood Pewee (*Contopus sordidulus*), birds called frequently but not more often or in a different manner during their breeding activity.

HABITAT PREFERENCE

The distribution pattern of the six vegetation groups is shown in figure 4. Figure 5 shows the location of all birds seen perched or in flight during the study. Each dot represents one bird, but individual birds were recorded only once during each census. Such a relative density map is a fair representation of the location of birds during the morning hours of the breeding season. Comparing figures 4 and 5, it is obvious that the stream area was most densely populated.

Study quadrats with high (> 30) or low (< 5) bird densities were determined and then classified by vegetation type. The occurrence of high bird densities differed significantly ($\chi^2 = 42.49$, $P < 0.001$, 5 d.f.) among the vegetation types, but I found no

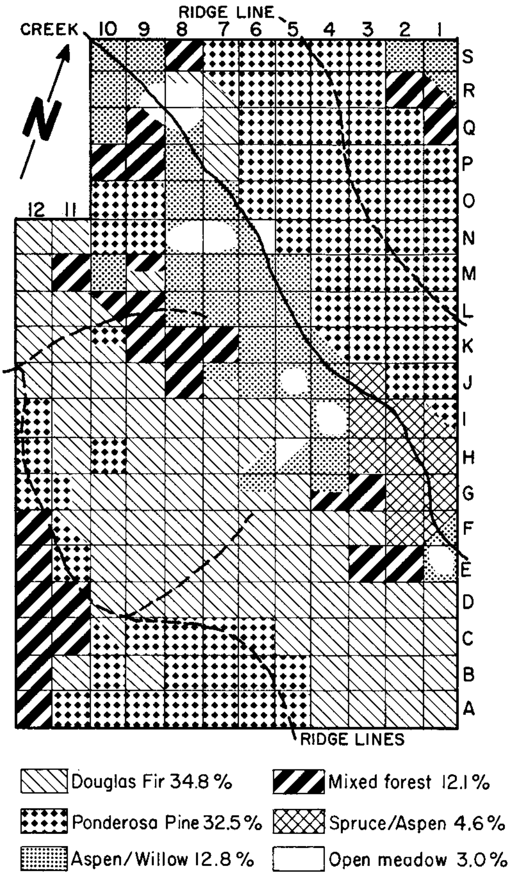

FIGURE 4. The distribution pattern of the six vegetation types in the study area, from 1967 to 1971.

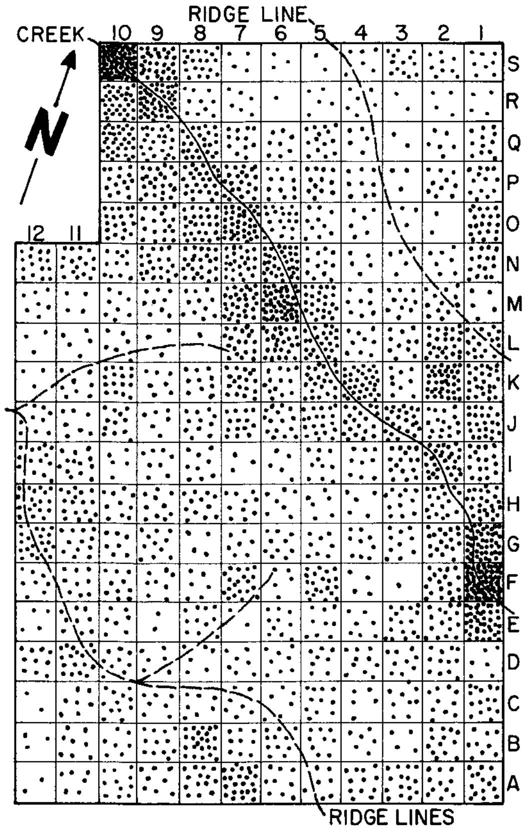

FIGURE 5. Bird distribution, as sampled during the morning hours of the breeding season, from 1967 to 1971. Each dot represents a bird seen perched or in flight in that location.

significant relationship between low bird densities and vegetation. In general, birds favored Aspen-Willow and Spruce-Aspen vegetation and did not favor Douglas Fir or mixed stands. Because bird densities in fir included many juvenile chickadees and juncos, although breeders were not usually found there, this difference is actually greater for breeding birds than is apparent.

Table 2 shows the percent occurrence of common bird species in the vegetation types in comparison with the abundance of those vegetation types. Where the percentage of time the bird spent in a vegetation type exceeds the percentage occurrence of that vegetation, some vegetational preference exists. Birds should have been easiest to see in open meadows, then in pine, fir, Mixed Forest, Aspen-Willow, and Spruce-Aspen. Thus the numbers of birds occurring in the two aspen categories were probably higher than are shown in table 2.

Figure 6 shows how habitat preferences changed within the year for each of the seven dominant species. Strength of preference is measured here by the size of the positive values resulting from the comparison of observed percentage with expected percentage of habitat use when testing for significance of vegetation use by each species. Because percentages were involved, the arcsin transformation was used. Only positive values (obs.-exp.) were depicted as negative values indicated avoidance of vegetation rather than preference for it. The Robin showed strong vegetational preference in each of the three time periods ($\chi^2 = 12.25$, $P < 0.05$; $\chi^2 = 31.12$, $P < 0.001$; $\chi^2 = 29.95$, $P < 0.001$, all 5 d.f. for March–May, June, and July–August, respectively). Aspen-Willow was preferred through the nesting season in June, and then the birds moved into Spruce-Aspen. Thus, the decreased numbers of Robins seen after June may indicate dispersal following the nesting season.

An early preference shown by the Broad-tailed Hummingbird for both aspen vegetations (fig. 3) lessened somewhat during the June nesting season. The preference for Aspen-Willow became stronger in July and

TABLE 2. Percentage of observations of the common bird species in the study area made in each vegetation type. Species exhibiting preference for a particular vegetation are bracketed.

Vegetation type % occurrence	Aspen-Willow 12.8%	Ponderosa Pine 32.5%	Open 3%	Mixed 12.1%	Douglas Fir 34.8%	Spruce-Aspen 4.6%
Bird Species						
Turdus migratorius	27%	36%	4%	14%	11%	8%
Cyanocitta stelleri	24	37	1.4	7	23.6	7
Parus gambeli	25.2	22.7	2	9	33	8
Troglodytes aedon	58	6	2.5	2.5	10	20
Selasphorus platycercus	30.5	28.2	6	9	21	5
Junco caniceps	28	24	2.7	13	21.3	11
Vireo gilvus	64	16		2	11	7
Tachycineta thalassina	43.8	3.2	4.6	1.6	1.6	45.3
Chlorura chlorura	42	6				51
Oporornis tolmiei	59	5	5		5	24
Regulus calendula	35.5	6.4	3	13	16	26
Dendroica coronata auduboni	41	15	2.4	2.4	30.8	10
Dendrocopus villosus	30	15	30	5	15	5
Contopus sordidulus	67	17		8		8
Sialia mexicana	67	13			13	7
Sitta pygmaea	18	54	.5	11.5	15	1
Colaptes auratus	14	52		9	19	6
Sitta carolinensis		50			50	
Myadestes townsendi	20	48	1	12	19	
Nucifraga columbiana	10.4	59		6	22	1
Zenaida macroura		77		7	15	
Dendragapus obscurus	7.6	46		7.6	38.4	
Sitta canadensis	5	17		9	64	5
Certhea familiaris		11			89	
Empidonax difficilis	18	18		9	55	
Sphyrapicus thyroideus	20	16		12	44	8
Spinus pinus	7	20	3	9	49	12
Loxia curvirostra		38		32	23	7

August, a time of bloom for many montane flowering plants. Preference and avoidance were again strong for all three periods ($\chi^2 = 24.6$, $P < 0.001$; $\chi^2 = 14.44$, $P < 0.05$; $\chi^2 = 32.95$, $P < 0.001$, 5 d.f.). Pygmy Nuthatches showed strong and continued preference for Ponderosa Pine ($\chi^2 = 18.95$, $P < 0.01$; $\chi^2 = 35.23$, $P < 0.001$; $\chi^2 = 31.62$, $P < 0.001$, 5 d.f.). House Wrens showed the strongest habitat preference of the seven dominant species ($\chi^2 = 106.04$, $P < 0.001$; $\chi^2 = 84.25$, $P < 0.001$; $\chi^2 = 79.23$, $P < 0.001$, 5 d.f.) and favored both aspen vegetations throughout the breeding season. Mountain Chickadees and Gray-headed Juncos both showed a low but continued preference for Aspen-Willow which was least in July and August, when flocks of juveniles appeared in the Douglas Fir areas. Neither species showed significant preferences at that time ($\chi^2 = 9.0$, $P = 0.09$; $\chi^2 = 12.4$, $P < 0.05$; $\chi^2 = 4.8$, $P = 0.4$; and $\chi^2 = 17.4$, $P < 0.01$; $\chi^2 = 16.3$, $P < 0.01$; $\chi^2 = 8.7$, $P = 0.12$, 5 d.f.). Steller's Jays showed a moderate preference for Ponderosa Pine in their June nesting time, as well as a continuing preference for Aspen-Willow through the summer. Vegetation preference was significant only during June ($\chi^2 = 8.9$, $P > 0.10$; $\chi^2 = 19.29$, $P < 0.01$; $\chi^2 = 7.4$, $P > 0.10$, 5 d.f.). Again, numbers decreased after June (fig. 2).

VEGETATION PATCHINESS AND EDGE EFFECT

Because of the great numbers of birds in the aspen and the linear distribution of this vegetation, it may be edge effect that provides the attraction for birds. I made the following comparisons to try to determine if "edge" and the consequent proximity of several vegetation types, or the presence of aspen itself was more important to the birds. At two points in the study grid, four vegetation types merged (points EF 1–2 and MN 10–11, fig. 4). The first group of four included two aspen quadrats, and 146 birds were found there. The second group of four included one aspen quadrat and 47 birds. The 24 points where three types of vegetation merged were compared for bird density also; the number of birds they supported averaged 53. Those points containing aspen as one member of the vegetation stands (n = 16) had an average of 60 birds. Those not containing

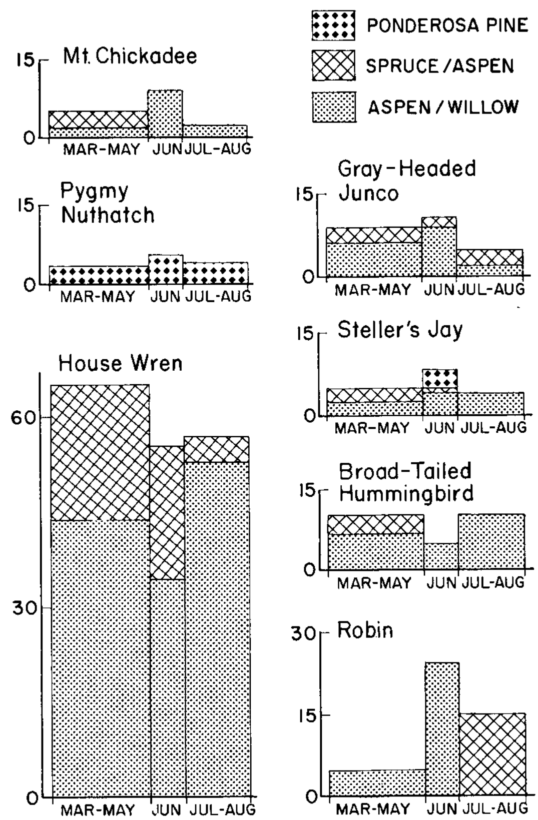

FIGURE 6. Habitat preference of the seven dominant species during the breeding season. Vertical axis measures strength of preference in units of (observed-expected)^2/expected. Only positive values were used. See text for explanation.

aspen (n = 8) averaged only 38 birds. In both cases the aspen areas showed higher relative densities than those attributable to merging vegetation alone. In nonparametric testing of edge with aspen against edge without aspen, the 24 points differed significantly (Wilcoxon Unpaired test, $P < 0.0056$, 2-tailed), indicating that aspen as a component of edge was enriching.

To compare densities within areas of homogeneous vegetation and those in patchy edge situations, groups of quadrats of Douglas Fir (n = 28) and Ponderosa Pine (n = 28) were compared to quadrats of Mixed Forest (n = 24). Both fir and pine samples contained no "edge" other than that normally found in pure stands (see Discussion). Mixed Forest quadrats were all in edge situations and, by definition, composed of patchy vegetation stands (fig. 4). These three samples did not differ significantly in average bird density ($\chi^2 = 1.79$, $P > 0.05$, 2 d.f.). In all, densities were below average.

TABLE 3. Results of bird censuses[a] in montane areas of the Front Range of Colorado, summarized by habitat.

Habitat	No. studies	$\bar{x}$ No. prs/40 ha	No. species
Ponderosa Pine, below 1800 m	13	105	11
Ponderosa Pine, above 1800 m	6	193	24
Douglas Fir	8	143	11
Spruce-Fir	5	157	
Deciduous	6	314	26
Mixed Forest	6	226	24

[a] Data taken from Hering 1948, 1958, 1961, 1962, 1963, 1965, 1966, Lawhead 1949, D. Snyder 1950, Thatcher 1951, 1952a,b, 1953a,b, 1954a,b, 1955a,b, 1956, Cassel 1952, Beidleman 1960, M. Snyder 1968, 1969, 1970.

DISCUSSION

BIRD SPECIES AND REAL DENSITY

The total of 93 pairs of breeding birds/40 ha, distributed among an average of 22 breeding species and 11 visitor species was low. Udvardy (1957) reviewed 56 North American bird surveys and found species numbers to vary from 7 to 39, with densities of 150 to 500 pairs/40 ha. He added that lowest densites were found in western pine woods. Fifty species were seen in Crow Gulch in the five year period, but only 78% of these were seen in any one year. The number of Crow Gulch species was then relatively high, but densities were low.

Censuses in the southwest, such as those of Tatschl (1967) in New Mexico, and Balda (1969) in Arizona, reported higher numbers of both species, 24 to 35, and pairs, 150 to 759/40 ha, in the different types of vegetation. Results of northern censuses also were higher; Salt (1957) reported 1045 birds/40 ha in flatland aspen of Wyoming, and Manuwal (1968) listed 143 to 200 pairs/40 ha in Montana Douglas Fir. Results of Colorado censuses were more similar to mine (table 3). They indicated that montane bird densities are generally lower in Colorado than elsewhere in the west, at least along the Front Range. The species found in this study compare well with all western studies. Wauer (1964) gave the altitudinal ranges of many birds in the Panamint Mountains of California. All match my data except his report of Yellow-rumped Warblers, Common Flickers, and Western Bluebirds (*Sialia mexicana*) not breeding below 3080 m, which they commonly do in Colorado. Differences in moisture could cause this.

My first hypothesis, that most breeding species show constant density levels from year to year, was supported by the densities of the dominant species (table 1). These birds represented over 50% of all breeding pairs. The number of all breeding species remained nearly constant, but the total number of breeding pairs for all species rose. This can be explained partly by a real increase in the numbers of three species and partly by increased observer knowledge of the area and what constitutes a breeding pair. The breeding pair concept is difficult to delimit. Singing males can be considered as members of a pair or as surplus males. Kendeigh and Baldwin (1937) estimated that the number of non-breeding House Wrens constituted up to half the local population. Polygamous species, like the wren, and species in which females alone rear the brood (e.g., Broad-tailed Hummingbird and Blue Grouse, Bent 1932, 1940) do not fit the usual breeding pair picture. As an observer becomes familiar with the territories and learns to recognize the behavioral cues denoting pair formation in the various species, the accuracy and efficiency of census work increases. Therefore, data collected after the first year were probably more complete. For this reason I excluded my 1967 data from densities depicted in figure 1.

RELATIVE AVIAN DENSITIES

The density estimates I made in each census of the last four years of the study allowed analysis of the change in bird numbers within the year (Hypothesis 2) because I conducted each census in the same manner, and because the grouped four-year data provided enough samples for each month ($\bar{x} = 8$) to be meaningful. A seasonal increase in total number was found among dominants (fig. 2), as well as in all birds seen (fig. 1). Some species, like the jay and Robin, decreased in numbers as the season progressed (fig. 2). As both these species reproduced successfully in the area, their early high numbers and later low numbers must represent some sort of population movement. Their actual densities (table 1) were determined by counting territories which were best observed during active nesting. Thus, the breeding density of Steller's Jay is best reflected by numbers in late May (fig. 3). For the Robin, the breeding density covers the period from mid-June to early July.

TEMPORAL SPACING OF BREEDING

Figure 3 shows the wide spacing of breeding activity within the season (Hypothesis 3). Most activity occurred in June. If species numbers are converted to standing biomass, by multiplying the numbers of a species by average weight of individuals, the two greatest peaks of activity occurred the first weeks of both June and July. Consuming biomass, which reflects metabolic rate as well as size, peaks at the same times. Total biomass was distributed so that at one time, actively nesting birds never represented more than 58% of it. Data also indicate that the feeding habits (as described by Schoener 1968, and Salt 1957) of synchronously breeding species showed the same diversity and spacing as did biomass.

Nesthole competition is an aspect of montane breeding activity not well understood. However, because woodpeckers are responsible for the holes in which non-drilling species nest, the nesting activities of Downy (*Dendrocopus pubescens*) and Hairy (*D. villosus*) woodpeckers, Williamson's Sapsucker (*Sphyrapicus thyroideus*) and Common Flickers are potentially limiting to the Mountain Chickadee, House Wren, Western Bluebird, and Violet-green Swallow. The woodpeckers also are helpful to the three nuthatch species, which can do some excavating in decayed wood, and probably also to each other in providing suitable nestholes. Thus, the spacing of species nesting activity shown by the woodpeckers (fig. 3) may be important. Only woodpecker holes in the aspen were used by the other species. Pygmy Nuthatches nested in holes in dead pine stubs, but it was not clear whether woodpeckers started these holes. Approximately one third of the aspen or dead pine stubs where nestholes were found one year were broken off or fallen the following spring. Thus the continual drilling by the woodpeckers seems necessary for the existence of the other hole-nesters, and the number of woodpeckers may in part determine the numbers of the other species. Trees selected by the woodpeckers for drilling often seem to be infected by fungus, the apparent reason why the trees break off or fall.

Competition for a nesthole was observed in 1968, and it is possible that the spacing of breeding activity may be affected by such struggles. A pair of Western Bluebirds evicted a pair of Violet-green Swallows from the nesthole the swallows had used previously and were reoccupying for the season. The bluebirds reared their young and left the area in early July. The following week a pair of swallows began nesting in the same tree in a hole 60 cm below the contested one. The next spring the tree was broken off, with both nestholes on the ground. Immelman (1971) discussed nestholes as possible limiting factors. It is likely they are important as such in Crow

Gulch, but as less than 50% of the breeding species use nestholes, other, more important factors must exist as well.

HABITAT PREFERENCE

Definite preferences for Aspen-Willow and Spruce-Aspen vegetation were shown by most Crow Gulch birds, and Mixed Forest and Douglas Fir were least preferred. The existence of such preferences was predicted by Hypothesis 4. Salt (1957) found Wyoming aspen forest to be richest in birds of all montane vegetation he studied. It was 10 times richer than coniferous forest. Tatschl (1967) found New Mexico aspen also showed the highest bird density. Engstrom (1955) and Williamson (1970) reported an enriching effect of groves of deciduous trees among conifers. The habitat preferences listed for the various species match fairly well with other reports (Tatschl 1967).

Possible reasons for habitat preferences are suggested by comparing the change in preferences shown by the dominant species (fig. 6) with their nesting periods (fig. 3). Strong preference for a vegetation often coincides with its use for nesting. The House Wren's strong preference for aspen in all seasons correlates with a very long nesting period during which aspen nestholes were utilized. Chickadees, which also nested in aspen holes, preferred aspen most strongly during their June nesting season. Most Pygmy Nuthatches nested in dead pine, and their preference for pine was greatest during their two nesting periods. However, the other dominants nested in the open in other vegetation and still preferred aspen, whether nesting or not. This indicates that aspen held some attraction for them other than nest sites. Food availability may be that attraction.

Aspen vegetation differs from the other types in Crow Gulch in that it is deciduous and slow to leaf out in the spring. Therefore, a deep understory of forbs, herbs, and grasses begins to grow in May and is fully developed by July when the aspen are in full leaf. I began sampling insects in this layer in 1973. Data indicate high numbers, but more importantly, great diversity of species. Because most nestlings are fed insects (Lack 1968), the aspen groves form a good source of food. This, and the aspen nestholes required by some species may be the factors governing aspen preference. If food availability strongly controls habitat preference and bird numbers, then low bird densities in the Front Range of Colorado may be due to low overall productivity. Perhaps primary productivity is limited by the dry climate ($\bar{x}$ pptn. = 59.8 cm/year at 2770 m near Crow Gulch, R = 40.4–67.0 cm). The occurrence of aspen in stream or spring areas also indicates that water levels may control both aspen distribution and resultant bird numbers.

VEGETATION PATCHINESS AND EDGE EFFECT

Hypothesis 5 is more difficult to analyze. North American ornithologists have long tried to measure bird populations in pure stands only, omitting from censuses any edge influence, although more birds usually are found in such areas (Johnston 1947). European ornithologists have emphasized work in representative areas, not in pure stands (Oelke 1966). The area I studied contained large pure stands of Douglas Fir (7 ha) and Ponderosa Pine (6 ha). It was also truly representative of montane vegetation.

In any stand, small openings occur because of fallen trees, soil conditions, or topographic irregularity. In Ponderosa forests, mature trees often are separated by large expanses of grass, in contrast to dense thickets of young pine. Does, then, more "edge" occur in the mature forest than in a young one? As a stable forest should contain both young and old trees in some sort of dynamic balance, edge effect should normally differ from place to place within any pure stand. For these reasons the European attitude toward census work seems more realistic.

Statistical analyses showed that high bird densities are strongly vegetation-dependent, but low densities are not. Also, edge containing aspen has a more important influence on bird density than just edge itself. Densities in homogeneous stands of fir and pine which excluded any edge, did not differ significantly from densities in patchy stands of Mixed Forest in edge situations. In all, densities of birds were below average; fir had the lowest, then Mixed Forest, then pine. Every test made in this small study area indicated that aspen vegetation strongly influences bird density.

MacArthur (1971) described how environmental patchiness controls density through the interaction of such factors as competition, nesting space availability, soil, topography, climate and microclimate, seral stage, climax vegetation and edge effect. Schoener (1968) emphasized that patchiness of food may allow higher density levels of herbivores and omnivores. In this study patchiness is best exhibited by Mixed Forest, itself a product of topographic, edaphic or microclimate changes. Fewest birds were found there.

CONCLUSION

The five hypotheses all are supported by the results of this study. That densities and habitat preference change within a breeding season, and that breeding activities of the bird fauna as a whole are spread over a long time, indicate that the traditional number of breeding pairs per unit space per year is, at best, an average of species and numbers. Continuing surveys are needed to provide a true picture of species balance.

The spatial and temporal separation of some species has been linked to food specialization and division of food resources (Edington and Edington 1972). Not enough is known about temporal differences in food habits of Crow Gulch species to make that statement, but food availability does seem to govern habitat preference and is suspected of controlling temporal changes in breeding activity and density. Bird species diversity in Crow Gulch was moderate, but bird numbers were low. If food availability and primary productivity are the controlling factors, then they limit bird numbers rather than species diversity.

SUMMARY

Avian density averaged 93 pairs/40 ha, representing an average of 22 breeding species and 11 visitor species yearly. Although 50 species were seen in the area, only 78% of these were present in any one year. Most breeding species showed constant yearly densities, and the seven dominant species totalled over 50% of the breeding pairs. Relative density of most species changed within the breeding season. Some species increased in numbers while others decreased. High relative densities were strongly related to vegetation type while low densities were not. A temporal spacing of nesting activity by the different species indicated a partitioning of the breeding season. It also reflected subdivision of food resources and feeding manner. Woodpecker numbers may limit the densities of other hole-nesting species. Bird species showed strong vegetational preferences, especially for aspen. Fewest birds were found in Douglas Fir and Mixed Forest. Edge and patchiness did not seem to raise relative densities. Tests indicated aspen itself was responsible for high density. Aspen areas probably support most birds because of high food availability and the presence of nest-holes.

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