

SUMMER BIRDS OF A LODGEPOLE-ASPEN FOREST IN THE SOUTHERN WARNER MOUNTAINS, CALIFORNIA

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The Warner Mountains occupy a narrow strip approximately 15 km wide and 160 km long running north and south in extreme northeastern California and southeastern Oregon. Geologically the range is the westernmost of the basin ranges which file eastward into Nevada and Utah and is characterized by tilted fault blocks of lake bed sediments interbedded with volcanic sediments and basalt (Oakshott 1971). In contrast, affinities of its boreal avifauna lie most closely with the adjacent Sierra Nevada and Cascade Ranges (Miller 1951, Johnson 1970). The flora of the Warner Mountains is largely a mosaic of Great Basin and Sierra Nevada forms (D. Taylor pers. comm.). Summers in the range are hot and dry with occasional and local thunderstorms, and winters are cold with relatively sparse precipitation in at least the southern portion. Little has been published on the birds of the Warner Mountains (Johnson 1970, 1975; Maillard 1927; Miller 1941, 1951). Distributional data and indications of relative abundances of species present are scattered and incomplete. The interrelationships of the bird species and the influences which the area's unique geography and flora have had on bird communities in the range are just beginning to be explored. During the summer of 1975 a mapping census was carried out on the birds of a decadent stand of Lodgepole Pine (*Pinus contorta*) and Quaking Aspen (*Populus tremuloides*) in the Skunk Cabbage Creek drainage of the extreme southern Warner Mountains. The study was undertaken to gather data on bird distribution in the southern area of the range and the importance of various habitat types to individual bird species.

STUDY AREA AND METHODS

The Skunk Cabbage Creek study area (Figure 1) consisted of 27.2 ha (about 67 acres) in the southernmost forested area of the range (41° 10'N, 120° 10'W). The plot was a rectangle 594 m long and 457 m wide, the long side of which faced southeast into the small valley through which Skunk Cabbage Creek flows. The study area ranged in altitude from 2390 m up to 2450 m. The long axis of the plot ran approximately parallel to the contour of the area, and the average slope was an estimated 15%.

The forests in the Skunk Cabbage Creek area are generally patchy and broken with hillsides of sagebrush (*Artemisia*) interspersed with mule-ears (*Wyethia*) and lupines (*Lupinus*). The low areas around the creek are dominated by perennial bog vegetation with clumps of willows

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(*Salix*) and often extensive areas of corn-lily (*Veratrum*). The soils on the higher areas are generally light, sparse and very rocky, whereas the soils of the creekside bogs and meadows are dark and heavy. The Skunk Cabbage Creek area has had a history of relatively little disturbance. The major habitat alteration has been periodic summer grazing, and the

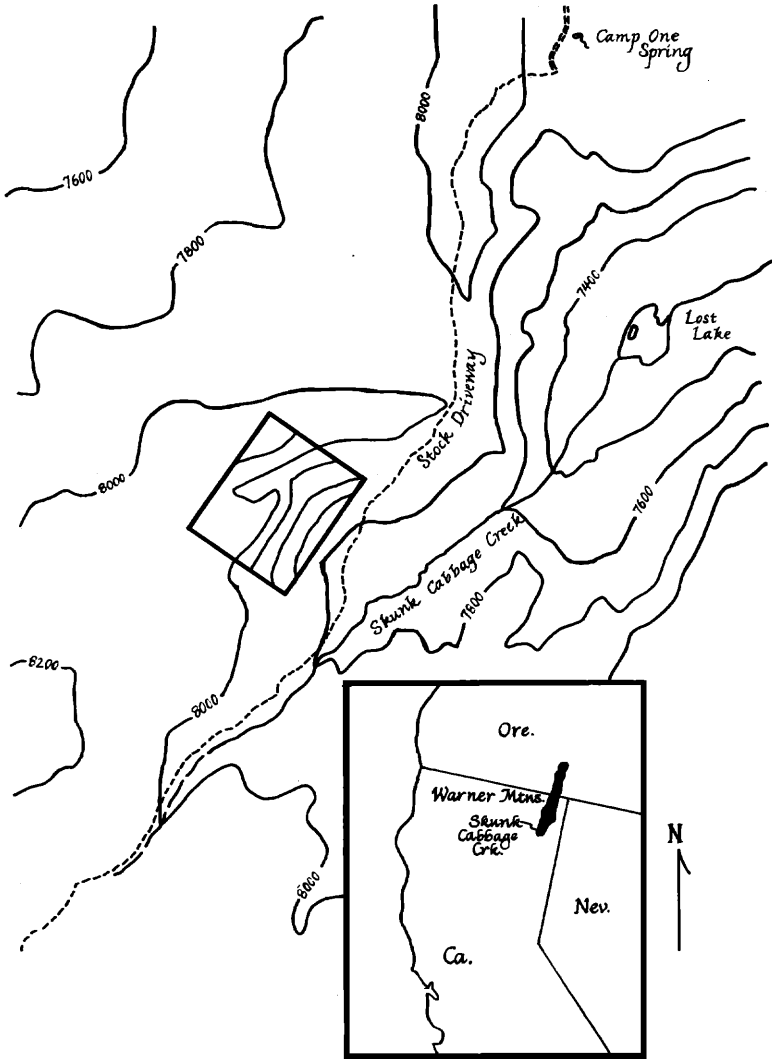


Figure 1. Location map of the Skunk Cabbage Creek study plot. Contour intervals within the plot boundary are forty vertical feet.

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area has not been logged. In the early 1960s a stock driveway was constructed up the valley just downslope from the present study area. There has not been a major fire in the area for at least 130 years.

Vegetation types on the plot (Figure 2) were classified as to percent composition of Lodgepole Pine and Quaking Aspen. Each vegetation type was further described by the techniques proposed by Emlen (1956) by sampling at randomly chosen sites within areas of each vegetation type. (Copies of these more detailed descriptions are available from Winkler on request.) Although our initial description of the vegetation used seven different categories of vegetation, several of these classes were lumped together for use in analysis of the bird populations on the plot. The following brief descriptions pertain to these lumped categories.

Lodgepole Forest (9.0 ha, 33% of total vegetation cover): Pure stands of lodgepole are the densest habitat on the plot, with limited visibility, little sub-canopy light and no appreciable ground cover. As aspen occurs in greater proportions, the lodgepole forest becomes more open with sparse ground cover and a shallow litter layer.

Mixed Forest (5.4 ha, 20% of cover): Forest with approximately equal proportions of aspen and lodgepole is heterogenous in aspect, with tall pines interspersed freely with stunted aspen. Ground cover and litter layers are better developed here than in the lodgepole forest.

Aspen Forest (9.5 ha, 35%): This vegetation occurs in two different types of potential significance to avian habitat selection. The dense aspen is the least extensive of the two and is characterized by apparently healthy trees growing to 6-7 m in height and forming a continuous canopy. The open aspen is more common and seems to be the type from which the aspen components in mixed habitats are derived. Ground cover is best developed in the closed aspen and is very sparse in open aspen. Large amounts of litter are found in both habitats, reaching a maximum in open aspen where the density of downed trees and slash often makes walking difficult. The trees in the open aspen are typically sickly in appearance; their foliage is often sparse and pale in color. Insect infestations often reach epidemic proportions in stands of this type. The principal insect pest appears to be the larvae of the tortricid moth, *Sparganothis californiana*. By mid-July a large number of the trees in the open aspen were shedding many leaves, apparently due solely to insect infestation.

Sagebrush (3.0 ha, 11%): This habitat is typically composed of heavy stands of *Artemisia*, often with considerable *Wyethia* and *Lupinus*.

Open Areas (0.3 ha, 1%): In this habitat the substrate is almost continuous rock and the predominant vegetation is low herbs. This designation is used for areas with small sagebrush plants as long as the sagebrush is not dominant. Even with the latter provision, the distinction between

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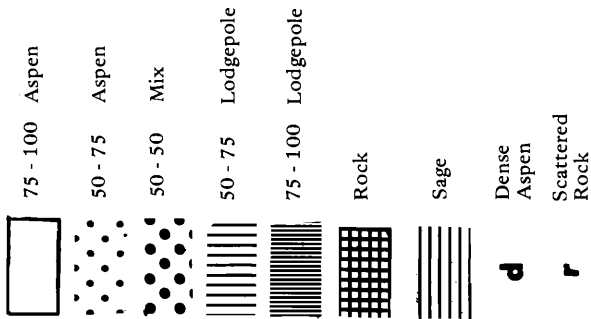
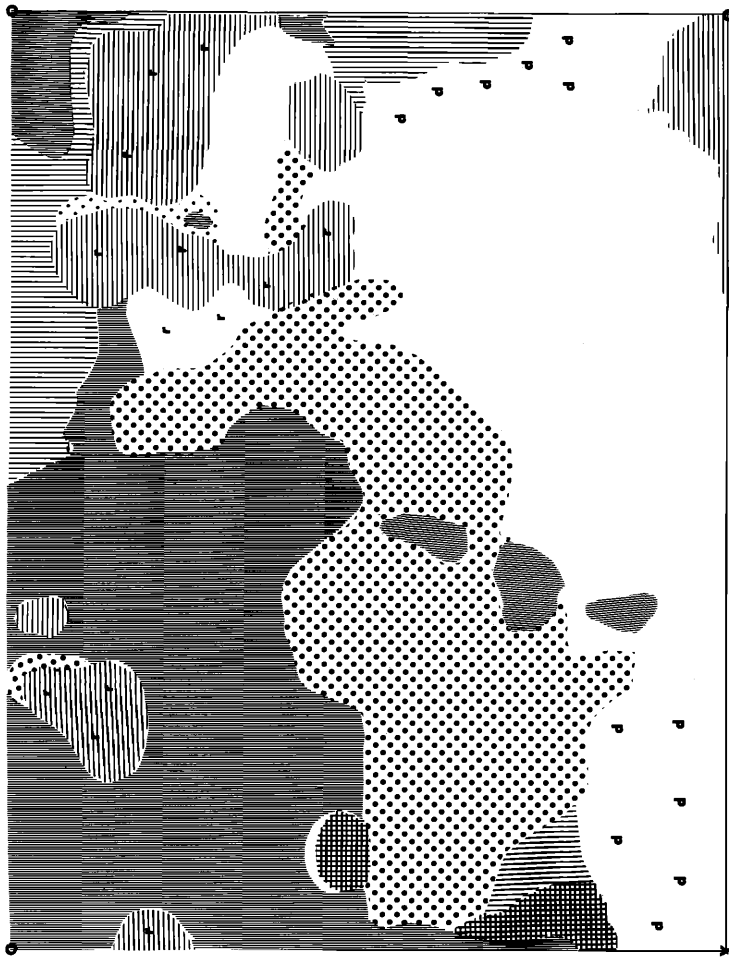




Figure 2 (above): Vegetation map for the Skunk Cabbage Creek study plot. See text for vegetative type descriptions.

Figure 3 (right): Territories of Brewer's Sparrow (thickest lines), Chipping Sparrow (intermediate lines) and Dark-eyed Junco (thinnest lines) on the Skunk Cabbage study plot.

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open areas and other vegetation types is often unclear, and in the initial description of the vegetation we resorted to the use of such categories as "rock-sage" and "rock-aspen" in an attempt to express the intermediate nature of certain areas of vegetation.

A grid of 46 m squares was superimposed on the plot by marking the corners of each square with a coded combination of plastic surveyor's tape. Censuses were conducted by walking leisurely along rows between grid markers and recording each contact on a tracing paper overlay of the plot grid. The overlay was marked with a unique symbol for each species and accessory symbols for the behavior in which the bird was engaged (see International Bird Census Committee 1970). A running summation of the location and number of all contacts for all species was maintained. To maximize coverage time during the most productive morning hours and to minimize inequalities in observer coverage, the census was usually divided between two observers who alternated halves of the plot each day. An equivalent of ten censuses were conducted between 30 June and 26 July. Each census involved an average of about six observer hours.

Most species for which sufficient data were collected could easily be categorized by habitat preference and/or the approximate number of breeding pairs on the plot based on superimposition of the species map on the vegetation map. At least three species presented problems in analysis due to their ubiquitous and abundant occurrence. These species, Pine Siskin, Evening Grosbeak and Red Crossbill, were analyzed by determining the number of contacts for each species in each habitat type.

RESULTS

Table 1 presents a list of bird species encountered on the Skunk Cabbage Creek study area along with categorizations of ecological characteristics and avifaunal affinities for each. The categorizations of foraging and predominant food are taken from Johnson (1975:557) or from Bent (1937-1968). When more than one food is listed, the first listed is deemed to be of predominant importance to breeding birds of the species.

Designations of residence and migratory status are based on Maillard (1927) and Grinnell and Miller (1944). The abbreviations and their interpretations are as follows: "LV" represents local visitors, species that are thought to have bred in the vicinity and visited the plot during or immediately after breeding. "MV" designates migrant visitors, species that bred distant from the plot and only visited the plot in the course of their annual migrations. "B" represents birds that are thought to have bred on the plot. "R" is used to signify species that probably stay on or very near the plot throughout the entire year. "AM" represents altitudinal migrants, those which migrate to contiguous lower elevations

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in winter. Some altitudinal migrants may leave the breeding grounds only when conditions are severe enough to force them away. "M" signifies species that are latitudinal migrants and typically leave the area for wintering areas to the south before the onset of severe climatic conditions or food limitations. These classifications are among the most subjective made in the study, for little is known of the winter movements of birds in the Warner Mountains, and it is often difficult to characterize the migratory patterns of all individuals in a population with a single designation.

The approximate number of pairs per km² was estimated by computing the number of pairs per ha of the species' preferred habitat and multiplying by one hundred.

The "hole-nesting" category includes only species that nest in cavities in trees. Although a Rock Wren nested in a stump cavity, this species is not treated as a hole-nester, for it typically nests in holes among rocks (Bent 1948).

The determinations of avifaunal affinities are based on the lists in Miller (1951) and Johnson (1975).

Habitat preferences were determined by evaluation of the species maps superimposed on the vegetation map. As should be evident from Table 1, the analyses carried out on the Pine Siskin, Red Crossbill and Evening Grosbeak revealed no habitat preferences. Habitat preferences are indicated in Table 1 in the following manner. Habitat types for which a species is judged to exhibit primary habitat preference are indicated by X's appearing in columns beneath the habitat type headings. Numbers in parentheses indicate the number of records in a habitat type when there are very few records. The X's for Lazuli Bunting and White-crowned Sparrow are intentionally placed in an intermediate position between sage and aspen in an effort to express the interface nature of the preferred habitat of these two species.

Table 1 (cont.)

SPECIES	FORAGING	FOOD	STATUS		Residence	Migratory	Pairs/km ²	Avidity	Hole-nesting	Lodgepole	HABITAT			
			M	AM							Mix	Aspen	Sage	Open
Brown-headed Cowbird <i>Molothrus ater</i>	Ground	Insects	B	M	19	Aus	—	—	—	—	X	(1)		
Western Tanager <i>Piranga ludoviciana</i>	Tree foliage	Insects	B	M	35	Brl	—	—	X		X			
Black-headed Grosbeak <i>Pheucticus melanocephalus</i>	Tree foliage	Insects, seeds	MV									(3)		
Lazuli Bunting <i>Passerina amoena</i>	Tree foliage	Insects, seeds	LV										X	
Evening Grosbeak <i>Hesperiphona vespertina</i>	Tree foliage	Insects, seeds	B	AM	29	Brl	—	—	X		X			
Cassin's Finch <i>Carpodacus cassinii</i>	Tree foliage	Seeds, insects	B	R	67	Brl	—	—	X					
Pine Siskin <i>Carduelis spinus</i>	Tree foliage	Insects, seeds	B	M	67	Brl	—	—	X		X			
Red Crossbill <i>Loxia curvirostra</i>	Tree foliage	Insects, seeds	BP	R	29	Brl	—	—	X		X			
Green-tailed Towhee <i>Pipilo chlorura</i>	Ground-brush	Insects, seeds	LV									(1)		
Dark-eyed Junco <i>Junco hyemalis</i>	Ground-brush	Insects, seeds	B	AM	42	Brl	—	—	X		X			
Chipping Sparrow <i>Spizella passerina</i>	Ground-brush	Insects, seeds	B	M	60	Aus?	—	—			X			
Brewer's Sparrow <i>Spizella breweri</i>	Ground-brush	Insects, seeds	B	M	133	Aus	—	—						X
White-crowned Sparrow <i>Zonotrichia leucophrys</i>	Ground-brush	Insects, seeds	B	M	33	Brl	—	—						X

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SPECIES ACCOUNTS

The assignment of any species to a restricted habitat type is somewhat subjective. The following notes for selected species clarify the evidence for each determination and provide additional details.

RUFIOUS HUMMINGBIRD: Observed around the major concentrations of nectar-bearing plants from 9 July on. No adult males were observed.

CALLIOPE HUMMINGBIRD: Appeared with the first large concentration of hummingbirds on 19 July.

WILLIAMSON'S SAPSUCKER: Nested in an aspen grove approximately 6 km north of the study plot at Patterson and probably nested adjacent to the plot.

BLACK-BACKED THREE-TOED WOODPECKER: Probably nested in the pure lodgepole forest west of the plot. This species occurred on the study plot in November 1974 (H. Newhouse pers. comm.). This observation, coupled with the fact that our only record for this species on the plot was on 21 August suggests that this species may shift its feeding activities into aspen areas following the breeding season.

EMPIDONAX SPP.: No members of this group were examined in the hand; therefore, no definite specific identifications were made. On the basis of appearance, behavior (type of tail wag) and call note, we strongly suspect that *E. wrightii* was present in the lower sage-aspen areas. Two *Empidonax* nests were found in the upper lodgepole forest on the branches of Lodgepole Pines less than 2 m off the ground. These nests probably did not belong to the *wrightii*-like individuals which we observed predominantly in the lower aspen and were very likely the nests of *oberholseri*.

TREE SWALLOW: Visitor to open aspen only. Probably nested adjacent to the plot and known to nest in aspen at Patterson, 6 km to the north.

CLARK'S NUTCRACKER: Only seen flying over the plot or once perched high in a Lodgepole Pine. Probably nested in the alpine country to the north and visited the area after breeding, for this conspicuous species was not seen until 21 July.

ROCK WREN: One nest with three young was found in an aspen stump on the extreme northeastern corner of the plot on 25 July. This pair presumably spent most of its time out of the plot, as this was the only date the species was observed in that part of the area. The other two pairs were restricted to rocky openings in the lodgepole and mixed forests. A Rock Wren was observed singing from the limbs of a Lodgepole Pine approximately 10 m off the ground on 20 July.

AMERICAN ROBIN: Four nests were found, all in aspens about 3 m off the ground. One with two eggs and one with three eggs on 9 July, the latter with two young by 19 July. A third nest had three young on 22 July. The contents of the fourth nest were not examined. This species seems to be reliant on openings in the forest for nesting.

MOUNTAIN BLUEBIRD: Two of the five pairs nested in dense aspen and moved into open aspen feeding their young once the young had fledged.

WARBLING VIREO: Two nests found adjacent to the plot: One about 8 m up in a 10 m aspen and one near the top of a 2 m aspen. The latter had two eggs in it on 10 July, both of which were apparently robbed, as the nest was abandoned by 20 July.

LAZULI BUNTING: Occurred in the open aspen on the northeastern corner of the plot, first appearing 18 July. The singing male in this area was probably a post-breeding wanderer from localities to the north or downslope (Erickson 1968, Pough 1957).

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CASSIN'S FINCH: This species tended to move into the lower areas of open aspen as the summer progressed. During the last census periods many of the contacts for this species in the open aspen involved adult birds in the company of small groups of fledglings.

PINE SISKIN: Although this species was seen in small groups (3-5 individuals) throughout the breeding season, there is no reason to doubt the likelihood of its breeding, for territorial defense is very lax in this species (Palmer 1968), and the circling flights of males were observed.

RED CROSSBILL: No definite evidence of nesting was obtained for this exceptionally sporadic species. Although crossbills were observed in all forest types, it is probable that nesting activities, if any, were carried out in the lodgepole forest. The species was observed in large numbers throughout the census period, but large flocks (20-50 individuals) were not observed until 18 July. At least two apparently juvenal plumaged birds were observed in the company of at least one adult in an aspen in the open aspen area on 10 July. Breeding activity for the Red Crossbill has never been reported from the Warner Mountains (Johnson 1975).

DARK-EYED JUNCO: One ground nest found in open aspen contained four eggs on 10 July and on 20 July there were three young with one egg still unhatched.

CHIPPING SPARROW: A territorial encounter between this and the preceding species was observed in the lodgepole-mixed forest interface on 21 July.

BREWER'S SPARROW: Three of the four pairs occupied patches of sagebrush, whereas the fourth occupied the most open area of the aspen with a conspicuous sagebrush understory.

In a study of finches in the mountains of southern California, Cody (1974: 231-240) hypothesized that similarities in the songs of the Dark-eyed Junco, Chipping Sparrow, and Black-chinned Sparrow (*Spizella atrogularis*) have evolved to maximize the efficiency of maintenance of interspecific territoriality between these species. Our data from the Warners (Figure 3) indicate that the territories of the Dark-eyed Junco, Chipping Sparrow, and Brewer's Sparrow are broadly overlapping in the Skunk Cabbage Creek area. The songs of the former two species were often indistinguishable, whereas the song of the Brewer's Sparrow was very distinctive. If the similarities in song between the junco and the Chipping Sparrow have evolved as a mechanism for the maintenance of interspecific territoriality, the mechanism does not seem to be working in the populations we studied.

WHITE-CROWNED SPARROW: A common breeder in the sage-meadow interface immediately downslope from the study area; only portions of two territories reached the plot. A female with a well-developed egg in the lower oviduct was captured and released on 9 July.

One unofficial census was made on the study area on 21 August. At this time flocks of White-crowned, Chipping, and Brewer's sparrows, all with young, were present in the lower open aspen area along with three Townsend's Warblers (*Dendroica townsendi*) and four Solitary Vireos (*Vireo solitarius*). Apparently, as the summer progresses and young are fledged, the lower aspen area takes on increased importance as a feeding area for both breeding birds and migrants. The major food item for many of these birds in the aspen was most likely tortricid moth larvae.

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Table 2. Potential indicators of community structure and function on the Skunk Cabbage Creek study plot. See text for details.

	HABITAT TYPE					
	Open	Sage	Aspen	Mix	Lodge-pole	Over-all
% latitudinal migrants	100	100	47	58	46	60
% latitudinal + altitudinal migrants	100	100	80	83	69	84
% tree cavity nesters	0	0	40	17	23	24
% primary insectivores	100	0	67	58	54	68
% Boreal affinity	0	50	79	82	100	75

Table 2 contains a habitat-specific breakdown of some potential indicators of community organization. In the computation of the values in this table, only those birds thought to breed on the study area are considered. The unidentified *Empidonax* flycatchers were left out of the computation of “% Boreal affinity”. We have considered primary insectivores to be those species which include insects or other invertebrates as a great majority of their diets during the breeding season. In the analysis of this character we have relied a great deal on published accounts, especially the classic series by Bent (1937-1968) and the recent work of Johnson (1975:557). It is possible that some of the finches should have been included in the category of primary insectivore in view of their propensity to take large numbers of invertebrate prey during times of peak invertebrate abundance and nestling protein demand.

Interhabitat avifaunal similarities were estimated by dividing the number of species shared by both habitats by the total number of bird species in both habitats. Similarity values were calculated both with (St) and without (Sp) five “generalist” species (Mountain Chickadee, Evening Grosbeak, Pine Siskin, Red Crossbill and Dark-eyed Junco). Similarity values for aspen and mixed forests (St=.42, Sp=.21), lodgepole and mixed forests (St=.53, Sp=.30), and lodgepole and aspen forests (St=.33, Sp=.13) were the only values greater than zero. The unidentified *Empidonax* were omitted in the calculations of similarity values.

DISCUSSION

In this study we chose a modified spot-mapping technique following the standards proposed by the International Bird Census Committee (op. cit.) because we were more interested in general spatial relationships than in absolute abundance (for the latter see Emlen 1971). We encountered several difficulties with the techniques we employed, including ambiguities in the code used for census grid corners and inability to see corner stakes on steep terrain with any appreciable ground cover. Another source of difficulty involves the coded designations used for vocalizations: it is best to determine from the outset precisely how each vocalization type in a species' vocal repertoire is to be recorded (e.g., whether as a flight call, territorial call, song, etc.). In the lodgepole and dense aspen forests, the very poor visibility of birds and grid corner markers may have introduced a bias in the data for some species. This is a factor which must constantly be kept in mind during use of the spot-mapping technique. Overcoming this obstacle would probably be possible if a grid with smaller squares was used, allowing a more thorough coverage of the habitat. Additionally, since many of the contacts registered in dense forest involve vocalizations, efforts should be made to proceed much more slowly in the dense areas of a plot.

The major deviation of our study from the majority of bird community studies is the lack of quantitative description of the vegetation. From the beginning we intended to correlate individual species distributions with habitats in only a general way. If more detailed correlations with specific habitat parameters are desired, the techniques employed by James (1971) and Anderson and Shugart (1974) seem to be the best yet developed.

Among the traits von Haartman (1957, 1971) associates with the hole-nesting habit is the tendency for hole-nesting birds to be residents. To meet intense competition for nest holes and potential nest sites, it is to the advantage of hole-nesting species to be present on the breeding grounds as early as possible. This prediction is upheld by our data, as only two (29%) of the seven hole-nesting breeders are migratory ("M" only). This proportion is well below the plot mean and the proportions for any of the other habitats. Flack (1976) and Lawrence (1967) have pointed out the importance of soft-wooded trees, especially aspen, for hole-nesting species. The drilling of nest holes is often impossible for many hole-excavating species in the trunks and branches of tree species with relatively hard wood. Flack has also indicated that hole-nesters will excavate cavities more readily in trees whose wood has been softened by insect infestation or disease. Lodgepole Pine has exceptionally hard bark (H. Newhouse pers. comm.). On the basis of these observations one would predict the highest proportion of hole-

nesting species to be in the aspen on the Skunk Cabbage Creek plot. This is precisely the relationship observed (Table 2).

The aspen contains proportionally more primary insectivores than do any of the other forested vegetation types on the plot (Table 2). Additionally, the highest number of species (15) occurs in the aspen. Deciduous forests harbor more invertebrates per weight of twigs than do coniferous forests (von Haartman 1971). This relationship, coupled with the observation that insects seemed to be more numerous in the aspen than in any other vegetation type during the summer of our study, tend to support the possibility that the higher proportion of primary insectivores in the aspen is a real response in the avifauna to higher prey concentrations in that habitat. Whether higher insectivore levels in the aspen is a condition to be expected every breeding season depends on whether prey levels in that habitat are equally high in all years and whether the insectivore populations respond to varying prey levels through differential fecundity or migration. It is interesting that Kingery (1970, 1971, 1973) reports higher nesting activity in lodgepole mixed with aspen than in pure lodgepole in a series of censuses from Colorado.

As winter comes to the study area, marked changes in the avifauna must result. With the ground covered with snow, the breeders in the open areas must leave, and it is not surprising that all the breeders from these areas are migratory. In the forested areas considerably more cover and above snow forage is available, and there is a reduced proportion of migrants. Additionally, many of the migrants in these areas are altitudinal migrants and possibly only leave the high country when weather and food conditions are at their worst. As cold weather approaches, insect populations collapse and most primary insectivores must leave: of the breeding primary insectivores, fifteen (88%) are either latitudinal or altitudinal migrants.

The similarities between the avifaunas of the different habitat types (see Results) are certainly not surprising, and they reinforce the notion that discontinuities in forest characteristics are perceived similarly by both birds and people.

Reviews of the birds of aspen forests (Flack 1976) and coniferous forest (Wiens 1975) of North America have recently appeared. Comparison with these reports on a species by species basis would be redundant, for, with minor exception, these accounts reinforce our conclusions regarding habitat preference. Comparisons with the work of Johnson (1975) have strengthened our impression that the avifauna of our study area is little different from that of comparable areas in the adjacent Sierra Nevada. This affinity with the Boreal avifauna of the west declines steadily from the fauna of the lodgepole forest down through the forested types and reaches a low in the open area avifauna. Not

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surprisingly, the open area avifauna has been derived from the surrounding Great Basin austral areas. It is interesting that many species known to breed in the northern Warners (e.g., Western Flycatcher, Gray Jay and Golden-crowned Kinglet) do not occur in areas of similar habitat in the southern part of the range. This observation suggests that these mountains may have been colonized by Boreal populations from the north and that the avifauna of the southern Warners is relatively impoverished.

The initial findings of this study have potentially significant land management implications. The decadent stands of aspen are apparently of great importance in maintaining the bird populations on the plot. Not only is aspen important as a source of potential nest sites for hole-nesting species, but it appears that the insect populations associated with the aspen are very important for both breeding birds and transients.

Aspen stands probably become more susceptible to disease and insect infestation as they grow older. As a result, it may seem senseless to many land managers to retain old and relatively unattractive stands of aspen which may act as potential reservoirs of infestation for neighboring stands. At least some decadent stands, however, must be maintained until land management personnel better understand the requirements of bird populations that aspen stands of varying ages can satisfy over the variations of the changing seasons and year to year fluctuations. Much the same considerations apply to lodgepole forest. The management of forests for heterogenous age composition should be given the highest consideration in weighing management alternatives until more is known about the relationship between bird populations and the state of their habitat.

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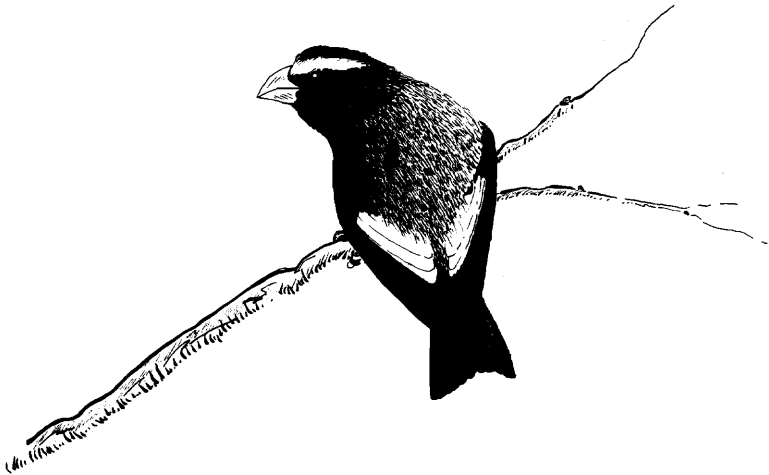
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