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SEASONAL CHANGES IN BIRD COMMUNITIES OF THE CHAPARRAL AND BLUE-OAK WOODLANDS IN CENTRAL CALIFORNIA[1]

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Abstract. During 1984 and 1985 we censused winter and spring bird communities in chamise, mixed chaparral, and blue-oak woodland habitats at Pinnacles National Monument, California. Both species composition and relative abundance of bird species in chaparral communities were more similar between seasons and years than were those of the oak woodlands. In all seasons species richness and bird numbers were highest in the blue-oak woodland, where the proportion of seasonal residents during the winter was similar to the chaparral but increased to over 37% in the spring. The number of granivorous species remained constant across habitats, but insectivores increased with increasing vegetation complexity. The high degree of variability in the blue-oak bird communities, relative to the chaparral assemblages, is probably due to greater variation in food resource availability between seasons and from year to year.

Key words: Avian community structure; seasonal turnover; California chaparral and blue-oak woodland habitat; avian censuses; species richness.

INTRODUCTION

The bird community in any given habitat type is not static but changes seasonally. Bird communities in temperate regions are comprised of a core of permanent resident species, complemented by winter and spring seasonal species, which combine to form varying communities throughout the year (e.g., Hilden 1965, Anderson 1972, Cordonnier 1976).

Comparisons among habitat types have shown that greater structural complexity of the vegetation generally leads to higher species richness and higher bird densities (e.g., MacArthur and MacArthur 1961, Emlen 1972, Balda 1975). But few studies in California have compared how seasonal changes in bird communities from the nonbreeding to the breeding season vary among habitat types. Cody (1974) described bird communities in two types of chaparral and in live-oak (*Quercus agrifolia*) woodland in the Santa Monica Mountains, California. He found little seasonal change in species richness in the oak woodland, where the number of wintering species was similar to the number during the breeding season. In contrast, species richness increased from spring to winter in the chaparral sites. Cody suggested that the persistent year-round community organization in the oak woodland may be more resistant to large numbers of winter invaders.

In 1984 and 1985, we censused birds in chaparral and oak-woodland habitats during the winter and spring at Pinnacles National Monument in central California. The objectives of our study were: (1) to describe relative abundance and composition of bird species in chamise, mixed chaparral, and blue-oak woodland communities at Pinnacles National Monument during the spring (breeding) and winter (nonbreeding) seasons; (2) to analyze seasonal differences in bird community composition; and (3) to determine the composition of avian foraging guilds between seasons in chaparral and oak woodland habitats at Pinnacles National Monument.

METHODS

STUDY AREA

Pinnacles National Monument encompasses approximately 16,000 ha in the Gabilan Mountain Range 65 km inland from Monterey, California. Chaparral habitat covers between 80–85% of the area (Webb 1969), with oak and mixed riparian

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woodland accounting for most of the remaining vegetation. There is a Mediterranean-type climate with cool, wet winters and hot, dry summers. Precipitation averages 42 cm annually, with about 80% occurring during the December-March period (National Park Service 1983).

Candidate sites for bird surveys were selected using a 1:12,000-scale vegetation map prepared from aerial photographs taken in August 1983. Criteria for candidate sites included vegetation type, size of the stand (at least 5 ha), distance from the center to the edge of another vegetation type (at least 75 m), distance to other sites (at least 100 m), and accessibility. We purposely restricted sites to those with no recent fire history in order to reduce variability due to plant age and structure. Thus, all sites had been unburned for at least 30 years; none had been grazed.

HABITAT PARAMETERS

After inspecting candidate sites, we selected 35 permanent study plots within three vegetation types. Vegetation measurements were made during each year of the study and details are available in Halvorson and Clark (1989). At all chaparral study plots, the linear distance covered by each shrub species and the amount of bare ground and rock were measured along a randomly placed 30-m transect. In addition, at 2-m intervals along the transect, a meter stick was dropped vertically through the vegetation and the following data recorded: canopy height, heights above ground that the meter stick touched live and dead vegetation, and litter depth. Vegetation cover in blue-oak woodland was sampled by recording the plant species intercepted by a vertically held 5-m rod at 2-m intervals along 25-m transects extending from the center of each study plot in each of the four cardinal compass directions.

The 14 plots of mixed chaparral (the most common vegetation type in the monument) were primarily composed of chamise (*Adenostoma fasciculatum*) and buckbrush (*Ceanothus cuneatus*) but included manzanita (*Arctostaphylos glauca* and *A. pungens*), flowering ash (*Fraxinus dipetala*), scrub oak (*Quercus dumosa*), California buckwheat (*Eriogonum fasciculatum*), and hollyleaf cherry (*Prunus ilicifolia*). Shrub cover averaged 82.1% (±11.2) and canopy height averaged 214 cm (±62). This plant community commonly occurs on north-facing slopes, and the ground cover includes annual grasses or ferns and other shade-tolerant native species.

The seven chamise chaparral plots were restricted to the dry south- and west-facing slopes throughout the monument. Chamise accounted for the majority of the shrub cover, 57.3% ± 20.0 (±1 SD), with buckbrush and California buckwheat the only other frequently encountered shrub species. Mean canopy height was 151 cm (±37). Most plots had a sparse ground cover of annual grasses.

The 14 blue-oak (*Quercus douglasii*) woodland plots occurred on hillsides throughout the monument and were variable in stand age and structure. The oaks were often interspersed with digger pine (*Pinus sabiniana*) or California juniper (*Juniperus californica*), with understory components of chamise, redberry (*Rhamnus crocea*), mountain mahogany (*Cercocarpus betuloides*), flowering ash, or buckbrush. In blue-oak woodland, shrub cover averaged 16.9% (±16.5) and tree cover 45.1% (±17.0). Introduced annual grasses dominated the herbaceous ground cover, along with a rich mixture of native forbs.

BIRD SURVEYS

Study plots had from one to six census stations, with a total of 66 throughout the 35 permanent plots. A minimum distance of 100 m was maintained between stations. Bird censuses were made using the variable circular plot technique (Reynolds et al. 1980). After arriving at a station, the observer allowed 1 min for the effects of disturbance to abate. The following data were recorded for the next 5 min: species of bird detected; manner of detection (aural or visual); estimated distance of the bird from the observer (to within 5 m); and, number of birds if a flock was detected. Counts started within 30 min of sunrise and were completed within 3 hr. No counts were made when wind speed exceeded 5 on the Beaufort scale or when it rained more than a drizzle because of detection problems. In order to eliminate observer variability, one person (MLA) performed all of the censuses.

A 5-min count period was used to reduce the possibility of double-counting individuals and the likelihood that birds entered or left the area during the count (Granholm 1983). It has been shown that to describe bird community composition, a 5-min count period is as effective as those of longer duration (Fuller and Langslow 1984).

Each of the 66 census stations was visited 12 times, three times during each of the following

TABLE 1. Mean number of species and individual birds recorded at chaparral and blue-oak woodland plots during winter and spring of 1984 and 1985 at Pinnacles National Monument, California.

Season	Chamise chaparral (n = 7)	Mixed chaparral (n = 14)	Blue-oak woodland (n = 14)
	Number of species (±1 SD)		
Winter 1984	7.0 (1.8)	7.4 (2.1)	8.9 (1.6)
Spring 1984	8.3 (1.6)	10.2 (2.5)	15.8 (3.6)
Winter 1985	5.7 (1.5)	6.6 (1.8)	9.9 (3.6)
Spring 1985	6.3 (1.8)	8.2 (1.1)	14.0 (4.5)
	Number of individual birds (±1 SD)		
Winter 1984	18.9 (9.6)	15.3 (5.2)	24.0 (8.7)
Spring 1984	16.6 (5.0)	23.4 (10.7)	37.7 (12.8)
Winter 1985	12.4 (8.6)	10.9 (4.5)	37.0 (27.7)
Spring 1985	11.7 (4.4)	16.9 (5.8)	27.9 (12.5)

periods: 21 December 1983–22 February 1984; 2 April–5 June 1984; 23 November 1984–21 February 1985; and 2 April–27 June 1985. Fieldwork was scheduled so that no station was visited more than once every 2 weeks.

Bird species were assigned to one of three foraging guilds—nectarivore, granivore, or insectivore—based on Salt's (1953) classifications and supplemented by our field observations. The assignments reflect what we feel is the main foraging mode of each species. Scientific name, residency status, and foraging guild of bird species mentioned in the text and tables are given in Appendix 1.

DATA ANALYSIS

We computed relative bird densities from our census data following the fixed-radius point count method (Hutto et al. 1986). We chose this approach because of the difficulty in obtaining sufficient observations to generate detectability profiles for most species encountered, and because of the realization that relative density estimates were sufficient to meet our objectives. Thus, we used the number of detections within 50 m of the count point as the basis for our analysis.

We focused on differences in bird communities between seasons and habitat types. Because the same census stations were visited repeatedly during the study, it was possible to compare relative abundances using pair-wise analyses. For each habitat type, results from the counts within a season were combined to obtain mean values of bird numbers and species detected. Then, differences between seasons and years were examined with paired-comparison t-tests (Sokal and Rohlf 1969, p. 356). Spearman's rank correlation (Langley 1971) was used to test the similarity of species lists between seasons. The level of statistical significance was accepted when $P \leq 0.05$.

RESULTS

SEASONAL CHANGES OF BIRDS WITHIN HABITATS

Mixed chaparral. We found significant ($P < 0.05$) increases in numbers of species and birds detected from winter to spring in both years (Table 1). These increases were due primarily to influxes of seasonal birds. During the winter, seasonal species composed 27% of the community and in spring increased to 41% (Table 2). Numbers of seasonal birds also increased from 11% of the winter to 15% of the total spring detections. However, when examining interseasonal differences of the 10 most abundant species, the mixed chaparral was the most consistent habitat that we examined (Table 3: $r_s = 0.65$, $P < 0.05$). The Bewick's Wren, Wrentit, Rufous-sided Towhee, and Plain Titmouse ranked 1 to 4 in abundance, respectively, in both winter and spring. They comprised a stable core population that represented 54% of the total detections for both seasons.

Chamise chaparral. Each year the average number of species increased slightly ($P > 0.20$) while the number of birds detected decreased ($P > 0.20$) from winter to spring (Table 1). The percentage of seasonal species was the same as mixed chaparral (27% winter, 41% spring), but the total number of birds was slightly lower (9% winter, 13% spring). As in the mixed chaparral, eight species were common to both seasonal lists of the 10 most abundant (Table 4), but changing densities resulted in different interseasonal rankings ($r_s = 0.41$, $P = 0.21$). There was a spring disappearance of Dark-eyed Juncos, our second-ranked winter species, and an increase in Brown and Rufous-sided towhee numbers. The most consistent species in this habitat, Bewick's Wren, was top-ranked in both seasons and represented 27% and 17% of the winter and spring totals, respectively.

Blue-oak woodland. This was the most variable of the three habitats that we examined. Total species increased significantly ($P < 0.01$) from winter to spring each year (Table 1). The number of individuals detected in 1984 increased signif-

TABLE 2. Total numbers of seasonal and permanent residents detected in the winter and spring chaparral and blue-oak woodland bird communities at Pinnacles National Monument, California.

Habitat type	Residency status: Seasonal Winter	Seasonal Spring	Permanent Winter	Permanent Spring	Percent seasonal Winter	Percent seasonal Spring
Chamise chaparral						
Species	6	11	16	16	27.3	40.7
Birds	18	32	185	205	8.9	13.4
Mixed chaparral						
Species	7	13	19	19	26.9	40.6
Birds	50	80	400	450	11.1	15.1
Blue-oak woodland						
Species	8	24	31	31	20.5	43.6
Birds	60	347	630	571	8.7	37.8

icantly ($P < 0.01$) between seasons, but declined ($P > 0.20$) from winter to spring in 1985. Seasonal birds were more variable than in either of the chaparral habitats (Table 2). In the winter, seasonal species composed 20% of the avian community, while in spring they increased to 44%. The total number of individuals increased from 9% of the winter birds to 38% of the spring. Interseasonal examination of the 10 top-ranked species further attests to the variability in this habitat (Table 5). Only six of the 10 most common winter species were ranked among the top 10 spring species ($r_s = 0.11$, $P = 0.70$). There were substantial decreases in Scrub Jays and Bewick's Wrens during the spring, coupled with an influx of four spring species. The 10 dominant species account for only 78% of the winter and 67% of the total spring birds, while in mixed chaparral they account for 90% and 78%, respectively.

SEASONAL CHANGES IN FORAGING GUILDS

Mixed chaparral. Granivorous species richness remained similar between seasons, with permanent species being double the number of seasonal species (Table 6). However, within the various species, numbers of permanent birds increased slightly during the spring, while seasonal bird detections decreased by more than half due to the loss of species such as the Fox Sparrow. Insectivores were more variable in this habitat

TABLE 3. The 10 most frequently detected species during 1985 and 1986 bird surveys in mixed-chaparral habitat at Pinnacles National Monument, California.

Species	Seasonal rank: Winter	Seasonal rank: Spring	% of total detections: Winter	% of total detections: Spring
Bewick's Wren	1	1	19.2	18.8
Wrentit	2	2	14.6	12.8
Rufous-sided Towhee	3	3	9.9	12.6
Plain Titmouse	4	4	9.9	9.9
California Thrasher	5	7	8.2	4.1
Fox Sparrow	6	—	8.0	—
Scrub Jay	7	6	7.7	4.1
Dark-eyed Junco	8	—	4.7	—
Anna's Hummingbird	9	10	3.8	3.7
Brown Towhee	10	8	3.6	3.9
Orange-crowned Warbler	—	5	—	4.5
Lesser Goldfinch	—	9	—	3.7
Totals			89.6	78.3

TABLE 4. The 10 most frequently detected species during 1985 and 1986 bird surveys in chamise chaparral habitat at Pinnacles National Monument, California.

Species	Seasonal rank: Winter	Seasonal rank: Spring	% of total detections: Winter	% of total detections: Spring
Bewick's Wren	1	1	27.4	17.0
Dark-eyed Junco	2	—	8.3	—
Wrentit	3	3	7.7	10.8
California Thrasher	4	5	7.7	6.2
Scrub Jay	5	9	7.7	3.6
Plain Titmouse	6	8	7.7	4.1
Anna's Hummingbird	7	6	7.1	6.2
Fox Sparrow	8	—	6.5	—
Brown Towhee	9	4	4.2	7.7
Rufous-sided Towhee	10	2	1.8	11.3
Rufous-crowned Sparrow	—	7	—	6.2
Ash-throated Flycatcher	—	10	—	3.6
Totals			86.3	76.6

TABLE 5. The 10 most frequently detected species during 1985 and 1986 bird surveys in blue-oak woodlands at Pinnacles National Monument, California.

Species	Seasonal rank		% of total detections	
	Winter	Spring	Winter	Spring
Plain Titmouse	1	1	18.5	12.1
Bewick's Wren	2	3	14.7	7.7
Scrub Jay	3	8	10.8	4.7
Rufous-sided Towhee	4	5	7.1	6.4
Brown Towhee	5	—	6.3	—
Dark-eyed Junco	6	—	4.7	—
Western Bluebird	7	9	4.5	46
White-breasted Nuthatch	8	10	4.0	3.6
Hutton's Vireo	9	—	3.4	—
Wrentit	10	—	3.4	—
House Wren	—	2	—	9.5
Violet-green Swallow	—	4	—	6.7
Ash-throated Flycatcher	—	6	—	5.9
Lesser Goldfinch		7		5.9
Totals			77.8	67.1

in that permanent species were 71% of the winter total but only 53% of the spring. Numbers of permanent insectivorous birds remained stable between seasons but there was a four-fold increase of seasonal birds in the spring. This spring increase was due primarily to the high numbers of Orange-crowned Warblers and Ash-throated Flycatchers.

Chamise chaparral. Patterns of granivorous species composition were the same as mixed chaparral (Table 6). The total number of granivorous birds were, however, much reduced in chamise due to lower numbers of Scrub Jays and Rufous-sided Towhees. This habitat also experienced a dramatic increase in seasonal insectivores during the spring with a doubling of species and a five-fold increase in total birds. The Violet-green Swallow, Ash-throated Flycatcher, and Orange-crowned Warbler were major contributors to this increase.

Blue-oak woodland. Permanent granivorous species numbers were the same between seasons, while seasonal species numbers more than doubled during the spring with the addition of species such as the House Finch, Black-headed Grosbeak, and Lawrence's Goldfinch. The total number of granivorous individuals that we counted within the community was similar between seasons because the increase in seasonal birds during the spring was offset by decreased numbers of permanent birds in such species as the Brown Towhee and Dark-eyed Junco during that census period. The most dramatic change of any foraging guild that we documented was the tremendous increase of spring seasonal insectivores into this habitat (Table 6). The number of species tripled while total birds detected went from 33 in the winter to 292 in the spring. This infusion of seasonal insectivores occurred in spite of the fact that numbers of permanent species and individuals remained little changed between seasons.

DISCUSSION

There is a striking seasonality to the avifauna at Pinnacles National Monument. The influx of seasonal birds during the late winter and spring greatly enriches the avian communities in all vegetation types. A portion of the seasonal variation that we recorded may be due to the differential detectability of some species. For instance, Scrub Jays are more secretive in the nesting sea-

TABLE 6. Residency status of granivorous (G) and insectivorous (I) species in the winter and spring bird communities in chaparral and blue-oak woodland study plots at Pinnacles National Monument, California.

Habitat type	Winter				Spring			
	Permanent		Seasonal		Permanent		Seasonal	
	G	I	G	I	G	I	G	I
Chamise chaparral								
Number of species	8	7	3	3	8	7	4	6
Number of individuals	59	114	13	5	86	109	6	25
Mixed chaparral								
Number of species	7	10	3	4	7	10	4	9
Number of individuals	136	250	35	15	160	271	13	67
Blue-oak woodland								
Number of species	9	15	3	5	9	15	7	15
Number of individuals	227	385	27	33	211	334	52	292

son and are, therefore, poorly censused using the variable circular plot technique (DeSante 1981). Because most of our detections were aural, it is also possible that changes in vocal behavior between seasons could contribute to higher spring numbers recorded for some species. However, even these possible biases cannot obfuscate the fact that a dramatic spring increase of species and numbers of birds occurred. The spring increase of species was consistent across all habitat types, going from 20% in the winter to over 40% in the spring (Table 1). Overall, we recorded 37 species during winter surveys compared to 59 species in the spring.

At Pinnacles, permanent residents dominated both the winter and spring chaparral communities. In contrast, spring residents such as the Ash-throated Flycatcher and Orange-crowned Warbler were among the numerically dominant birds in the blue-oak woodland and comprised over 37% of the total avifauna. The greater complexity of the oak woodland undoubtedly provided habitat for larger numbers of avian species and individuals as has been demonstrated in a number of other studies (e.g., Balda 1975). The woodland habitat is especially important to the birds at Pinnacles because it is relatively scarce. Chaparral habitat covers over 80% of the monument, so the significance of the oak woodland to avian populations is disproportionate to its abundance. Several species are virtually restricted to the blue-oak woodland habitat, with woodpeckers and nuthatches obvious examples. Others, such as the Ash-throated Flycatcher and House Wren, are dependent on tree cavities for nesting, even though they may forage in the more open shrub habitats.

We found an overall shift in bird communities toward greater insectivory in all habitats during the spring, as a result of an influx of spring seasonal residents. This increase was greatest in the blue-oak woodland. There is reason to believe that birds respond opportunistically to changes in available resources as seed supplies are depleted during the winter and invertebrates become more abundant in the spring (Rotenberry 1980). Although insectivorous species invaded all habitats in the spring, granivorous species and bird numbers were little changed between seasons suggesting a more stable component to the avian community structure at Pinnacles.

Comparison of winter and spring species lists of chaparral communities at Pinnacles, Santa Monica Mountains (Cody 1974), and Deep Canyon Desert Research Center (Weathers 1983) yields a grand total of 59 species, 23 of which are common to all three sites (Table 7). Despite physiographic and species differences, there is considerable similarity in the pattern of residency among species at each of the three locations. For example, all study areas had a core of permanent residents that composed approximately 50% of the avian community assemblage. Spring residents were consistently a greater percentage of the species and total birds than were winter residents. Moreover, insectivores dominated the spring seasonal species lists at each location. The greatest degree of species overlap is between Pinnacles and the Santa Monica Mountains, with a similarity index of 32/47 = 0.68. Pinnacles and Deep Canyon (0.52) and Deep Canyon and Santa Monica Mountains (0.44) exhibited considerably less overlap in species composition, probably due to elevational differences. Deep Canyon chaparral habitat is found between 1,400–1,800 m elevation, and of the 42 species at Deep Canyon, 12 were not recorded at the other two locations.

TABLE 7. Comparison of permanent and seasonal chaparral bird species at central and southern California locations.

Site	Number of resident species: Year-long	Winter	Spring	Total	Unique species
Pinnacles	24	6	13	43	5
Deep Canyon[a]	26	6	10	42	12
Santa Monica Mountains[b]	13	13	10	36	3

[a] Data from Weathers (1983).
[b] Data from Cody (1974).

The Pinnacles and Santa Monica Mountain sites are at 400–700 m elevation, and share many of the same species, although Cody (1974) found a higher number of winter species at Santa Monica. The more southern latitude of Santa Monica undoubtedly contributed to more winter species. But Cody lists several species (Canyon Wren, Lesser Goldfinch, Dark-eyed Junco) as winter residents that we found to be permanent residents at Pinnacles. Perhaps a more extensive sampling at a greater number of locations may have revealed these and other species to be permanent residents of Santa Monica Mountains.

At Pinnacles, species richness increased during the spring in each vegetation type during both years of our study, particularly in the blue-oak

woodland. Cody (1974) found less dramatic differences between seasons in Santa Monica where numbers of spring species in the chaparral decreased while they remained constant in the oak woodland. Cody (1974, p. 154–155) felt that: ". . . the increased equitability and predictability of the woodland permit a persistence of community organization year-round and a resistance by this community to large numbers of winter invaders." We found no evidence of this in the blue-oak woodland at Pinnacles. In fact, of the habitats that we censused, the blue-oak woodland had the greatest species differences between seasons (Tables 1, 5). The lack of concordance between our oak-woodland findings and Cody's may be partially due to differences in tree species composition and subsequent differences in the annual cycle of leaf fall and regrowth. The maintenance of leaf biomass in the live-oak woodland throughout the annual cycle, may create a habitat that would result in a more consistent avian community structure.

In summary, our findings indicate that the greater habitat complexity of the blue-oak woodland at Pinnacles does not necessarily promote greater constancy in the corresponding seasonal bird communities, but does lead to increased species richness. The chamise chaparral, which structurally and floristically is the least complex of the habitats that we examined, was less variable in bird composition than was the blue-oak woodland. In the deciduous blue-oak woodland, seasonal patterns of leaf and acorn production result in the periodic resource abundance that is exploited by an array of species. This, in turn, may cause greater turnover of species and less predictability in the bird community from season to season. Finally, each of these fluctuations results in a striking seasonality in the avian community structure at Pinnacles, that is similar in many ways to other chaparral and oak-woodland habitat in California, but also has components unique to the location.

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APPENDIX I. Common and scientific names, residency status, and foraging guild of bird species at Pinnacles National Monument, California, mentioned in this paper.

Common name	Scientific name	Residency[1]	Guild[2]
Anna's Hummingbird	*Calypte anna*	P	N
Ash-throated Flycatcher	*Myiarachus cinerascens*	S	I
Violet-green Swallow	*Tachycineta thalassina*	S	I
Scrub Jay	*Aphelocoma coerulescens*	P	G
Plain Titmouse	*Parus inornatus*	P	I
White-breasted Nuthatch	*Sitta carolinensis*	P	I
Canyon Wren	*Catherpes mexicanus*	P	I
Bewick's Wren	*Thryomanes bewickii*	P	I
House Wren	*Troglodytes aedon*	S	I
Western Bluebird	*Sialia mexicana*	P	I
Wrentit	*Chamaea fasciata*	P	I
California Thrasher	*Toxostoma redivivum*	P	I
Hutton's Vireo	*Vireo huttoni*	P	I
Orange-crowned Warbler	*Vermivora celata*	S	I
Black-headed Grosbeak	*Pheucticus melanocephalus*	S	G
Rufous-sided Towhee	*Pipilo erythrophthalmus*	P	G
Brown Towhee	*Pipilo fuscus*	P	G
Rufous-crowned Sparrow	*Aimophila ruficeps*	P	G
Fox Sparrow	*Passerella iliaca*	W	G
Dark-eyed Junco	*Junco hyemalis*	P	G
House Finch	*Carpodacus mexicanus*	P	G
Lesser Goldfinch	*Carduelis psaltria*	P	G
Lawrence's Goldfinch	*Carduelis lawrencei*	S	G

[1] P = permanent resident; S = spring resident; W = winter resident.
[2] G = granivore; I = insectivore; N = nectarivore.