

WEATHER AND BIRD POPULATIONS IN TRUE FIR FORESTS OF THE SIERRA NEVADA, CALIFORNIA¹

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Abstract. We monitored bird communities of true fir forests at 51 study sites in the western Sierra Nevada during the breeding seasons of 1983, 1984, and 1985. The summer of 1983 followed the El Niño winter of 1982-1983, with the greatest snowfall on record. The summers of 1984 and 1985 followed winters with moderate snowfalls. Bird species richness (BSR) and average total count (ATC) increased linearly from 1983 to 1985. The relative abundances of 12 common species increased from 1983 to 1985; abundances of two common species did not differ among years. Twenty-eight uncommon species increased and four decreased in numbers from 1983 to 1985.

Bird response patterns differed between lower-elevation white fir (*Abies concolor*) forests and upper-elevation red fir (*A. magnifica*) forests. Bird numbers were similar in both habitats in 1983 but greater in white fir than in red fir in 1984 and 1985. Although abundances of the common species increased in both habitats in both years, those of uncommon species did not increase substantially in red fir until 1985.

We suggest that bird numbers were depressed in 1983, but not atypically so for true fir forests. Numbers of permanent residents are often limited by frequent but unpredictable winters with excessive snowfall (Beedy 1982, Granholm 1982, Raphael and White 1984). Numbers of migrants, as in the case of this study, are sometimes affected similarly. White fir and lower-elevation forests may harbor "source" populations for red fir "sink" populations during periods of resource stress.

Key words: Bird community; bird assemblage; Sierra Nevada; El Niño; white fir; red fir; annual variation; *Abies concolor*; *Abies magnifica*.

INTRODUCTION

Birds vary annually (Holmes and Sturges 1975, Franzreb and Ohmart 1978, Szaro and Balda 1979, Järvinen 1980, Smith 1982, Rice et al. 1983a, Holmes et al. 1986) and seasonally (Winternitz 1976; Rice et al. 1980, 1983b) in distribution and local abundance. Järvinen (1979) and Noon et al. (1985) examined stability patterns of landbirds across Europe and North America, respectively. Stability was defined as: "... year-to-year persistence in species composition and distribution of species abundances" (Noon et al.

1985:64). Although Järvinen found that northern European bird communities were relatively unstable in comparison to southern Scandinavian and central European communities, Noon et al. found no such clear patterns among North American breeding bird communities according to habitat or geographic location. Noon et al. cautiously noted that, in general, grasslands showed greater annual variation in diversity than forested habitats, and within some habitats, northern communities were less stable than southern ones.

Weather seems to be an important factor in determining bird presence in montane communities of the Sierra Nevada. Beedy (1982) found substantial year-to-year variation in bird numbers in several coniferous forest bird communities in the western Sierra Nevada in California

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FIGURE 1. Study sites were located in the shaded areas on this map of California.

during 1976 to 1978. He noted declines of many resident species following the prolonged winter storms of 1977–1978. Raphael and White (1984) documented high negative correlations between yearly changes in cavity-nesting bird density and annual precipitation in eastern Sierra Nevada forests from 1966 to 1979. Preliminary results from our study in true fir forests of the western Sierra Nevada (Hejl and Beedy 1986) demonstrated similar annual variations in bird numbers between 1983 and 1984. Wiens (1974) suggested that the number of breeding birds that can successfully persist in grassland habitats is limited by large, recurrent, but unpredictable, variations in climate. Is weather similarly important in determining the number of species that inhabit montane forests?

The objectives of this study were (1) to characterize annual variations in bird species richness (BSR), average total count (ATC), the average count of common and uncommon species, and individual species' abundances in true fir forests, (2) to compare species composition between white and red fir habitats, (3) to characterize patterns of immigration and emigration (i.e., species turnover) within true fir forests, and (4) to determine relationships between winter snowfall patterns and bird population changes in white and red fir forests.

METHODS

STUDY SITES

We chose an extensive approach to studying bird distribution in the true fir forests of the western Sierra Nevada. These forests are composed of white fir (*Abies concolor*) stands at lower elevations and red fir (*A. magnifica*) stands at upper elevations; mixed stands are found at intermediate elevations. Canopy cover (Beedy 1981) and age of stand (Beedy 1982) could be important determinants of the presence of bird species in Sierra Nevada true fir forests. We studied a large number of sites within these forests to provide a wide range of canopy conditions within mature to old-growth stands.

Fifty-one study sites in true fir forests in Sequoia National Park (16 sites), Sierra National Forest (24 sites), and Yosemite National Park (11 sites) were randomly selected from 161 found (Fig. 1). All sites met the following criteria as determined by visual inspection: (1) most of the trees (> 2 m tall) were true fir; (2) situated in a stand of trees that was homogeneous in terms of age structure and canopy cover; and (3) located in stands at least 10 ha in size with dimensions accommodating a rectangle of at least 200 × 400 m. These stands were selected to obtain a wide distribution of canopy covers and age structures. Sites were selected in clusters of two or three that were sufficiently close to permit completion of bird counts in all between 05:30 and 11:30 PDT. In an attempt to assure independent assemblages, all sites were at least 400 m apart and most were 800 m apart. One sampling unit, or study site, was located in each stand.

BIRD OBSERVATIONS

One observer—the same for all 3 years of the study—recorded all birds seen or heard at each study site twice during the breeding seasons of 1983, 1984, and 1985, between 23 May and 30 July. A second observer—a different person each year—counted birds at all sites once each summer. Each site was visited during three different times of the day each summer—early morning (06:00 to 08:00), midmorning (08:00 to 09:30), and late morning (09:30 to 11:00) PDT. Birds were not counted during rain, high wind (> 34 km/hr), or snow.

At each site, a randomly placed transect 200 m long and at least 100 m from any edge or

discontinuity in the stand was chosen in the summer of 1983. The same transect was used in 1984 and 1985. The transect was marked with metal tags on the tree trunk nearest to each counting point and by hanging surveyor's flagging every 33 m between counting points. Counting points were located at the beginning, middle, and end of each transect; birds were also counted along the entire length of the transect. Observers recorded each bird using the stand, regardless of its distance from the observer. The sex and age of each bird, any breeding evidence, bird use of the stand, the first cue by which it was detected, and whether it was a new or repeat detection during that visit were recorded. Birds that were more than 100 m away were so noted in 1984 and 1985; however, few such detections occurred (pers. observ., SJH). An 8-min point count was made at the first point, followed by a slowly walked transect to the midpoint; another 8-min point count was done at the midpoint, followed by another slow walk along the transect to the end point; and a third point count was made at the end point. We tallied all adult birds detected, endeavoring to avoid double-counting individuals as we proceeded from point count to transect to point count. The transect was then walked slowly in the reverse direction. During that return walk, the observer recorded only those species that had not been detected earlier during that visit to the site, and those data were used only to compute BSR. All detections of adult birds that were determined to be using the stand, except those from the final walk, were used in the abundance analyses. Abundance values for common species separately, common species pooled, uncommon species pooled, and all species combined (ATC) were the average numbers of adults of each category detected on each site each summer. Detectabilities clearly differed among the species; however, we believe that these counts adequately reflect average abundance values across species for each site. We know of no obvious detectability differences that varied systematically between habitat types or years that may have contributed to the observed patterns.

Because our objective was to study a large number of sites within true fir forests, we compromised on the number of times we could visit each plot. Results from only three visits per summer probably underestimated the total bird community. Therefore, our calculations of BSR, ATC,

the combined abundances of the common species, the combined abundances of the uncommon species, and individual species' abundances are useful as relative indices for comparative purposes across our sites only, not as exact numbers for comparison with other studies.

VEGETATION MEASUREMENTS

To assess percent crown volume by tree species, 10 points were randomly picked from 36 points evenly spaced at 3-m intervals over each of six randomly placed 15- × 15-m plots, for a total of 60 points per site. From each point, an imaginary vertical column 1 m in diameter was projected upwards. If a tree was included within the column, the heights at which the column entered and left the tree foliage were estimated and recorded. If the column passed through a vertical gap >6 m within a tree, the two parts of the tree were treated as two trees. The crown volume of the trees was estimated by summing the lengths that were traversed by the imaginary column and multiplying that sum by the horizontal area of the column. Crown volume was calculated from the data and used to determine if a site was dominated by red or white fir. If greater than 50% of the true fir foliage volume was white fir, a site was considered to be dominated by white fir, and vice versa for red fir. Other vegetation measurements are described in our bird-habitat relationships work (Hejl 1987).

ANALYSES

Only breeding birds were analyzed. Raptors, aerial feeders, and ravens were excluded, as our methods precluded adequate counts of them. Breeding status was determined by direct evidence found on or near the study sites (nests, fledglings, or the presence of constantly singing males) or data from others who have studied these species in the same habitats (Grinnell and Storer 1924, Grinnell and Miller 1944, Verner and Boss 1980, Beedy and Granholm 1985).

For all statistical analyses, Dusky and Hammond's flycatchers (*Empidonax oberholseri* and *E. hammondi*) and Hairy and White-headed woodpeckers (*Picoides villosus* and *P. albolarvatus*) were each treated as one species. These two species-pairs were difficult to distinguish aurally, and the *Empidonax* flycatchers were also difficult to distinguish visually. Observer discrimination between these species increased each

year and we did not want this fact to influence the interpretation of results. Unfortunately, some information was lost by this procedure. However, some analyses were run both with and without the species lumped and our general results were statistically and biologically similar in each case.

To examine changes in species composition among years, we used the term "immigrant" for a species that was present in one year on a site where it was absent the year before and the term "emigrant" for a species that was absent in one year on a site where it was recorded the year before. The numbers of immigrants and emigrants were not merged into a turnover value, because, in our opinion, we lost information about community dynamics by doing so.

Analyses of variance were used to examine differences in BSR and the abundance patterns of all species, common species pooled, uncommon species pooled, and the common species separately among the 3 years. The randomized complete-block design included year as the treatment and site as the blocking factor (Steel and Torrie 1960:132–139, Snedecor and Cochran 1980:256–257). Histograms of the residuals looked symmetrical, unimodal, and approximately bell-shaped. Significant ANOVAs were followed by contrasts for linear trends (Steel and Torrie 1960:222–229). Paired *t*-tests were used to examine differences in the numbers of immigrant and emigrant species between successive years in the same habitat. Two-sample *t*-tests were used to examine differences in BSR, species' abundances, and immigrant and emigrant numbers between red and white fir sites.

"Common species" were those for which the mean abundances from all 51 study sites exceeded one detection per visit during at least two of the summers. This group included 14 individual species and the *Empidonax* and *Picoides* species-pairs for a total of 16 common species (Table 1). All other breeding species were "uncommon." We used ANOVA to analyze the abundances of the 14 common species in our among- and between-year comparisons. ANOVAs for individual species' abundances were treated as a family of comparisons. The significance levels for the 14 comparisons were adjusted with the Bonferroni inequality (Miller 1980:67–68). We could not examine statistically the abundance of each of the individual uncom-

mon species because our counts were too low. We arbitrarily set the significance level at 0.05.

SPECIES-ACCUMULATION CURVES

Species-accumulation curves were generated from cumulative BSR values calculated from each point, transect, or walk count to ascertain whether the three samples per summer were sufficient to detect most species that bred on each of our sites (Fig. 2). BSR increased throughout each summer's counts; however, the rate of accumulation slowed after the first visit. Because our methods were standardized, results should be adequate for between-site and between-year comparisons.

WEATHER

Snow-depth records from six California Snow Survey stations provided information on long- and short-term trends. These stations were located at Giant Forest (elevation 1,950 m) and Panther Meadow (2,621 m) in Sequoia National Park, Huntington Lake (2,133 m) and Nellie Lake (2,438 m) in the Sierra National Forest, and Peregoy Meadow (2,133 m) and Snow Flat (2,651 m) in Yosemite National Park. It is important to note that fieldwork for this study began during the summer immediately following the El Niño winter of 1982–1983.

ARTHROPOD SAMPLING

We collected samples of arthropods from tree foliage to estimate a rough index of arthropod biomass available to the birds in true fir forests, particularly foliage-gleaners. We sampled the tree foliage on six haphazardly selected study sites (from two study sites easily accessible early in 1983 in each of the three general areas of Sequoia National Park, Sierra National Forest, and Yosemite National Park). In 1983 and 1984, we obtained samples twice each summer on each of the six sites, and in 1985 on four of the sites. In 1985, two of the sites were sampled only in late summer. We clipped two 0.4-m samples of terminal foliage into a cloth insect net from 10 trees on each site; four of the trees were located near the first bird-counting point, three near the second, and three near the third. Each branch was shaken vigorously to dislodge arthropods inside a plastic bag. As did Brush and Stiles (1986), we observed few arthropods escaping and none failing to be dislodged. All samples were taken at

TABLE 1. Number of sites at which each species was recorded, by year and for all years combined. Species are ranked in descending order by the total number of sites at which each was recorded.

Species	1983	1984	1985	Total
Mountain Chickadee (<i>Parus gambeli</i>) ^a	49	51	51	51
Red-breasted Nuthatch (<i>Sitta canadensis</i>) ^a	50	51	51	51
Brown Creeper (<i>Certhia americana</i>) ^a	35	47	48	51
Golden-crowned Kinglet (<i>Regulus satrapa</i>) ^a	50	51	51	51
Hermit Thrush (<i>Catharus guttatus</i>) ^a	50	47	50	51
American Robin (<i>Turdus migratorius</i>) ^a	49	46	50	51
Yellow-rumped Warbler (<i>Dendroica coronata</i>) ^a	51	51	51	51
Western Tanager (<i>Piranga ludoviciana</i>) ^a	49	50	51	51
Dark-eyed Junco (<i>Junco hyemalis</i>) ^a	51	51	51	51
Pine Siskin (<i>Carduelis pinus</i>) ^a	45	50	50	51
Hammond's Flycatcher (<i>Empidonax hammondi</i>) ^b	35	41	47	50
Steller's Jay (<i>Cyanocitta stelleri</i>) ^a	44	43	48	50
Townsend's Solitaire (<i>Myadestes townsendi</i>)	42	38	37	50
Cassin's Finch (<i>Carpodacus cassinii</i>) ^a	45	49	45	50
Western Wood-Pewee (<i>Contopus sordidulus</i>) ^a	39	40	42	48
White-headed Woodpecker (<i>Picoides albolarvatus</i>) ^b	25	31	39	47
Northern Flicker (<i>Colaptes auratus</i>)	19	38	36	46
Dusky Flycatcher (<i>Empidonax oberholseri</i>) ^b	27	26	37	44
Evening Grosbeak (<i>Coccothraustes vespertinus</i>)	22	16	28	43
Red-breasted Sapsucker (<i>Sphyrapicus ruber</i>)	25	33	32	42
Chipping Sparrow (<i>Spizella passerina</i>)	26	22	35	42
Hairy Woodpecker (<i>Picoides villosus</i>) ^b	14	24	26	40
Fox Sparrow (<i>Passerella iliaca</i>) ^a	32	31	28	38
Mountain Quail (<i>Oreortyx pictus</i>)	15	18	20	36
Williamson's Sapsucker (<i>Sphyrapicus thyroideus</i>)	9	24	22	34
Warbling Vireo (<i>Vireo gilvus</i>)	18	21	27	33
Winter Wren (<i>Troglodytes troglodytes</i>)	14	18	29	32
Olive-sided Flycatcher (<i>Contopus borealis</i>)	17	19	24	31
Wilson's Warbler (<i>Wilsonia pusilla</i>)	9	7	29	31
Band-tailed Pigeon (<i>Columba fasciata</i>)	10	11	22	27
Clark's Nutcracker (<i>Nucifraga columbiana</i>)	9	13	16	26
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	3	15	16	25
Nashville Warbler (<i>Vermivora ruficapilla</i>)	3	15	19	25
Green-tailed Towhee (<i>Pipilo chlorurus</i>)	5	10	24	25
Western Bluebird (<i>Sialia mexicana</i>)	20	6	8	24
Hermit Warbler (<i>Dendroica occidentalis</i>)	10	18	13	24
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	7	15	9	21
Brown-headed Cowbird (<i>Molothrus ater</i>)	9	14	17	21
Red Crossbill (<i>Loxia curvirostra</i>)	16	14	4	21
Purple Finch (<i>Carpodacus purpureus</i>)	8	10	15	19
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	6	7	7	16
Pine Grosbeak (<i>Pinicola enucleator</i>)	5	3	12	14
Black-backed Woodpecker (<i>Picoides arcticus</i>)	3	3	11	12
Blue Grouse (<i>Dendragapus obscurus</i>)	5	5	5	11
MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	5	4	10	11
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	3	0	5	8
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	2	3	5	7
Calliope Hummingbird (<i>Stellula calliope</i>)	0	0	3	3
Mountain Bluebird (<i>Sialia currucoides</i>)	1	3	0	3
Swainson's Thrush (<i>Catharus ustulatus</i>)	0	0	1	1

^a Common species, i.e., mean counts of one or more detection per visit over all sites during at least two of the 3 years.

^b Each pair of the two flycatchers and the two woodpeckers is treated as a single common species.

midday (11:00 to 15:00) to reduce weather-related variability. After collection, insects were placed in ethyl alcohol for storage. In the winter of 1986–1987, insects were removed from stor-

age vials, air-dried for one day, and sorted into size classes. Each size class of insects from each sample was dried at 55°C for 30 hr; this time interval was predetermined to obtain a constant

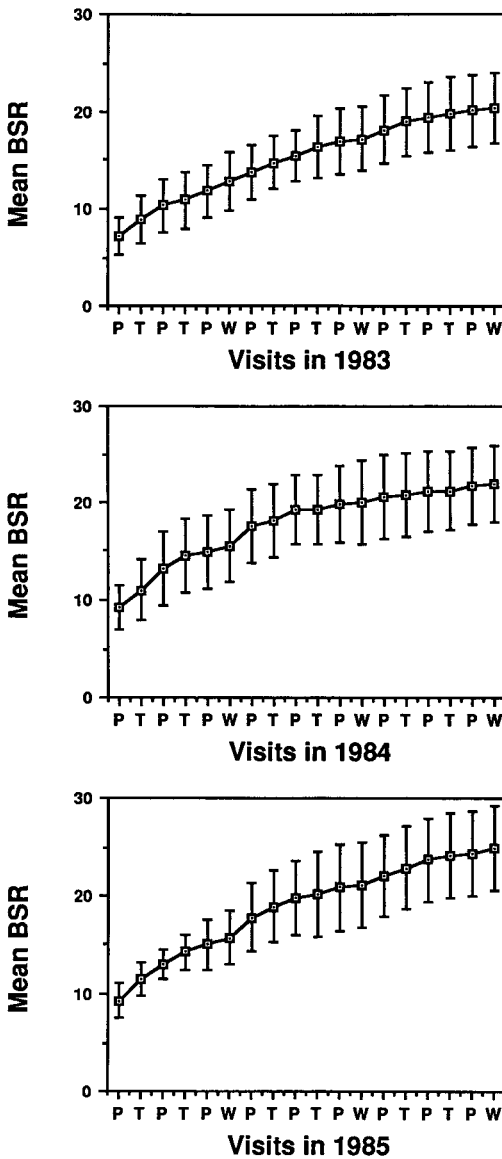


FIGURE 2. Species-accumulation curves by year. Curves connect average values of cumulative bird species richness (BSR) from 10 randomly picked sites at each bird-counting point (P), transect (T), and return walk (W). Three visits were made each summer; each visit is defined by the complete sequence P-T-P-T-P-W. Ninety-five percent confidence intervals for each value are shown with vertical lines.

weight of the largest sample. After each sample was removed from the oven, it was placed in a desiccator and quickly moved for weighing (to 0.0001 g) on a Mettler H15 balance.

TABLE 2. Yearly and total bird species richness (BSR) are listed by site, in descending order by total BSR. Area abbreviations: SNF = Sierra National Forest, SNP = Sequoia National Park, YNP = Yosemite National Park. Type abbreviations: WF = sites dominated by white fir; RF = sites dominated by red fir.

Site	Area	Type	1983 BSR	1984 BSR	1985 BSR	Total BSR
414	SNP	WF	31	36	35	39
413	SNP	WF	30	31	33	38
138	SNF	WF	23	25	30	37
155	SNF	RF	18	25	35	37
176	SNF	RF	20	22	30	37
417	SNP	WF	22	31	35	37
411	SNP	WF	24	32	32	35
412	SNP	WF	24	28	29	35
415	SNP	WF	29	29	32	35
154	SNF	WF	17	23	30	34
174	SNF	RF	22	24	32	34
318	YNP	WF	27	28	26	34
331	YNP	RF	23	24	32	34
418	SNP	WF	27	26	31	34
113	SNF	RF	17	22	28	33
171	SNF	RF	24	22	26	33
172	SNF	WF	23	28	26	33
306	YNP	RF	27	26	27	33
320	YNP	RF	23	24	25	33
126	SNF	RF	22	21	22	31
175	SNF	RF	22	19	28	31
177	SNF	RF	19	22	25	31
182	SNF	WF	23	27	26	31
404	SNP	RF	23	20	22	31
410	SNP	RF	22	18	24	31
317	YNP	RF	23	26	27	30
324	YNP	RF	23	23	23	30
333	YNP	RF	26	24	23	30
407	SNP	RF	24	25	21	30
153	SNF	RF	19	21	26	29
173	SNF	RF	21	23	25	29
321	YNP	RF	24	19	26	29
330	YNP	RF	21	23	26	29
401	SNP	RF	25	18	22	29
403	SNP	RF	20	21	23	29
416	SNP	WF	18	18	24	29
128	SNF	WF	20	25	21	28
129	SNF	RF	22	21	20	28
323	YNP	RF	20	18	27	28
409	SNP	RF	16	22	26	28
125	SNF	RF	20	19	22	27
178	SNF	RF	16	21	20	27
103	SNF	RF	16	18	22	26
130	SNF	WF	15	22	22	26
131	SNF	WF	17	23	21	26
450	SNP	RF	16	18	23	25
451	SNP	RF	16	19	19	25
104	SNF	RF	17	17	18	24
105	SNF	WF	13	19	22	24
163	SNF	RF	18	17	21	24
300	YNP	RF	18	18	14	23

TABLE 3. Results of randomized block-design analyses of variance on mean abundances of the 14 common species ($df = 2, 100$ in all cases).

Species	Source	F	P
Western Wood-Pewee	Year	9.57	0.0002
Steller's Jay	Year	7.26	0.0011
Mountain Chickadee	Year	14.85	<0.0001
Red-breasted Nuthatch	Year	128.64	<0.0001
Brown Creeper	Year	12.99	<0.0001
Golden-crowned Kinglet	Year	20.06	<0.0001
Hermit Thrush	Year	22.17	<0.0001
American Robin	Year	13.74	<0.0001
Yellow-rumped Warbler	Year	92.75	<0.0001
Western Tanager	Year	26.27	<0.0001
Fox Sparrow	Year	8.45	0.0004
Dark-eyed Junco	Year	1.38	0.2563
Cassin's Finch	Year	5.46	0.0056
Pine Siskin	Year	20.44	<0.0001

TABLE 4. Contrasts indicating linearly increasing population trends for the 12 common species with significant F s, according to ANOVA ($df = 1, 100$ in all cases).

Species	F	P	% explained*
Western Wood-Pewee	15.72	<0.0001	82
Steller's Jay	14.51	0.0002	100
Mountain Chickadee	28.86	<0.0001	97
Red-breasted Nuthatch	257.22	<0.0001	100
Brown Creeper	19.99	<0.0001	77
Golden-crowned Kinglet	40.12	<0.0001	100
Hermit Thrush	43.42	<0.0001	98
American Robin	11.50	0.0010	42
Yellow-rumped Warbler	181.74	<0.0001	98
Western Tanager	49.49	<0.0001	94
Fox Sparrow	12.49	0.0006	74
Pine Siskin	37.63	<0.0001	92

* Approximate percent of year sum of squares explained by the contrast.

RESULTS

DIFFERENCES AMONG YEARS

Bird species richness. We detected 50 breeding bird species during the summers of 1983 to 1985. Ten were present during at least one summer on all study sites (Table 1). Yellow-rumped Warblers and Dark-eyed Juncos (see Table 1 for scientific names) were present on all sites in all summers. At the other extreme, the Swainson's Thrush was found on only one site in only 1 year.

Total BSR—the number of species seen on a site during the 3 years combined—varied from 23 to 39 (Table 2). Maximum and minimum BSR within any summer were 36 and 13, respectively. BSR varied from year to year on each site but was correlated between years (1983 vs. 1984: $r = 0.66$, $df = 49$, $P < 0.001$; 1983 vs. 1985: $r = 0.48$, $df = 49$, $P < 0.001$; 1984 vs. 1985: $r = 0.69$, $df = 49$, $P < 0.001$).

Mean BSR was 21.3, 23.0, and 25.6 in 1983, 1984, and 1985, respectively. Differences were significant ($F = 32.13$; $df = 2, 100$; $P < 0.0001$) and increased linearly from 1983 to 1985 ($F = 63.20$; $df = 1, 100$; $P < 0.0001$).

Species' abundances. ATC of all species differed among years ($F = 193.92$; $df = 2, 100$; $P < 0.0001$) and increased from 35 individuals per site in 1983 to 45 in 1984 and 56 in 1985 ($F = 387.69$; $df = 1, 100$; $P < 0.0001$). Abundances

of the common species pooled increased linearly from 1983 to 1985 ($F = 385.28$; $df = 1, 100$; $P < 0.0001$), and mean abundances of 12 of the 14 common species separately differed among years (Table 3); abundances of all 12 increased linearly from 1983 to 1985 (Table 4). Abundances of only Dark-eyed Juncos and Cassin's Finches were not significantly different among years.

The pooled abundances of the uncommon species also increased linearly from 1983 to 1985 ($F = 69.41$; $df = 1, 100$; $P < 0.0001$). Individually, 28 uncommon species increased in numbers from 1983 to 1985. Four—the Western Bluebird, Mountain Bluebird, Townsend's Solitaire, and Red Crossbill—decreased in numbers.

Immigration and emigration. The mean number of immigrant species varied from five per site in 1984 (95% confidence intervals = 4.2–5.5) to six in 1985 (95% confidence intervals = 5.2–6.9), while the mean number of emigrants was rather constant at approximately three species per site (95% confidence intervals = 2.6–3.7 in 1984 and 2.9–3.9 in 1985). Immigrants outnumbered emigrants in both 1984 and 1985 ($t = 3.51$, $df = 50$, $P = 0.0010$ for 1984 and $t = 5.20$, $df = 50$, $P < 0.0001$ for 1985). Most immigrants and emigrants were uncommon species—83% in 1984 and 89% in 1985.

TABLE 5. Percent change in number of sites at which each species was counted in each succeeding year. Species were listed only if found on 20% or more sites in at least one habitat type in 1984 (vs. 1983) or in 1985 (vs. 1984).

Species	1984		1985	
	White fir	Red fir	White fir	Red fir
Common species				
Western Wood-Pewee	24	-3	-11	12
Brown Creeper	18	26	0	3
Cassin's Finch	29	12	0	-12
Pine Siskin	29	0	0	0
Uncommon species				
Band-tailed Pigeon	0	6	18	21
Williamson's Sapsucker	18	35	18	-26
Northern Flicker	47	32	6	-6
White-breasted Nuthatch	41	15	-6	-3
Winter Wren	6	12	29	9
Warbling Vireo	24	-3	-12	21
Nashville Warbler	65	0	-24	21
Hermit Warbler	41	0	-29	0
Wilson's Warbler	-12	0	47	32
Green-tailed Towhee	12	3	41	24
Chipping Sparrow	12	-18	6	38
Pine Grosbeak	0	-3	6	21
Evening Grosbeak	-18	-12	29	21

DIFFERENCES BETWEEN WHITE AND RED FIR HABITATS

Bird species richness. BSR values differed among years between red and white fir sites. In 1983, 1984, and 1985, BSR averaged 22.5, 26.5, and 27.9 on white fir sites and 20.7, 21.2, and 24.4 on red fir sites, respectively. BSR on white fir sites was similar to that on red fir sites in 1983 ($t = -1.33$, $df = 22$, $P = 0.2000$) but exceeded BSR on red fir sites in 1984 and 1985 ($t = -4.36$, $df = 21$, $P = 0.0003$, and $t = -2.56$, $df = 29$, $P = 0.0160$, respectively).

Increased BSR in both forest types in 1984 involved both common and uncommon species (Table 5). Three common and five uncommon species occurred on at least 20% more sites in 1984 than in 1983 in white fir stands, while this was true of only one common and two uncommon species in red fir stands. However, only the Northern Flicker was detected on at least 20% more sites in both forest types in 1984. In 1985, only uncommon species contributed to substantial increases in BSR. Four species in white fir and eight in red fir were present on at least 20% more sites in 1985. Wilson's Warblers, Green-tailed Towhees, and Evening Grosbeaks increased their presence in both white and red fir. Contrary to the increasing trend, three species with greatest changes in 1984—Nashville and

Hermit warblers in white fir and Williamson's Sapsuckers in red fir—were found on fewer sites in those habitats in 1985.

Species' abundances. Common species' abundance patterns, but not those of uncommon species, paralleled BSR patterns in the two habitat types. ATC on white fir sites was similar to that on red fir sites in 1983 ($t = 1.83$, $df = 24$, $P = 0.0800$) and exceeded that on red fir sites in 1984 and 1985 ($t = 3.51$, $df = 23$, $P = 0.0020$; and $t = 3.64$, $df = 26$, $P = 0.0012$) (Fig. 3). Mean abundances of common species pooled were similar in both habitats in 1983 ($t = 1.55$, $df = 25$, $P = 0.1400$) and greater in white fir than in red fir in 1984 and 1985 ($t = 2.93$, $df = 27$, $P = 0.0069$; and $t = 3.61$, $df = 31$, $P = 0.0011$). The Red-breasted Nuthatch was the only common species whose individual abundance reflected this pattern (Table 6). The abundances of the uncommon species pooled differed statistically in all 3 years between white and red fir sites ($t = 2.20$, $df = 25$, $P = 0.0370$ for 1983; $t = 3.46$, $df = 19$, $P = 0.0028$ for 1984; and $t = 2.47$, $df = 20$, $P = 0.0230$ for 1985).

Annual population changes for all common species except the Hermit Thrush were the same in the two habitat types (Table 7). Although the majority of the common species had greater abundances in white fir than in red fir each year,

TABLE 6. Mean number of birds/site/visit, by habitat and year, for the 14 common species. WF = sites dominated by white fir ($n = 17$); RF = sites dominated by red fir ($n = 34$).

Species	Habitat	1983		1984		1985	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Western Wood-Pewee	WF	1.37	0.31	1.29	0.21	2.08	0.41
	RF	0.80	0.17	0.91	0.17	1.17	0.20
Steller's Jay	WF	1.16	0.23	1.31	0.29	1.78	0.34
	RF	0.83	0.16	1.27	0.18	1.58	0.23
Mountain Chickadee	WF	1.31	0.21	2.27	0.34	2.98	0.32
	RF	1.99	0.24	2.74	0.24	3.05	0.29
Red-breasted Nuthatch	WF	1.53	0.16	3.14	0.24	4.65	0.37
	RF	1.44	0.11	2.59	0.14	3.89	0.21
Brown Creeper	WF	0.73	0.15	1.41	0.19	1.12	0.14
	RF	0.50	0.09	0.90	0.12	1.07	0.13
Golden-crowned Kinglet	WF	3.35	0.22	3.75	0.20	4.22	0.21
	RF	2.75	0.27	3.29	0.19	3.82	0.27
Hermit Thrush	WF	1.14	0.21	1.88	0.27	2.04	0.29
	RF	1.31	0.12	1.49	0.17	2.33	0.19
American Robin	WF	1.61	0.24	1.45	0.19	1.96	0.20
	RF	1.19	0.13	0.90	0.13	1.71	0.16
Yellow-rumped Warbler	WF	5.94	0.33	8.26	0.45	10.14	0.45
	RF	6.58	0.22	8.96	0.27	10.15	0.32
Western Tanager	WF	2.49	0.23	2.92	0.25	3.63	0.30
	RF	1.46	0.17	1.71	0.16	2.51	0.16
Fox Sparrow	WF	1.86	0.38	1.90	0.36	2.65	0.47
	RF	0.68	0.21	0.65	0.22	0.94	0.32
Dark-eyed Junco	WF	5.26	0.43	5.92	0.48	5.92	0.38
	RF	4.59	0.28	4.86	0.32	4.79	0.30
Cassin's Finch	WF	0.73	0.19	1.47	0.21	1.04	0.15
	RF	1.26	0.18	1.76	0.21	1.57	0.26
Pine Siskin	WF	0.96	0.27	1.67	0.25	1.71	0.23
	RF	1.01	0.14	1.83	0.19	2.20	0.18

TABLE 7. Differences in mean abundances between years for the 14 common species. Two-sample t -tests compared differences in abundances of species (1984 minus 1983, 1985 minus 1984) in white fir (WF) with differences in red fir (RF) sites.

Species	1984 minus 1983					1985 minus 1984				
	WF \bar{x}	RF \bar{x}	t	P	df	WF \bar{x}	RF \bar{x}	t	P	df
Western Wood-Pewee	-0.08	0.11	0.73	0.47	24	0.78	0.26	-1.87	0.07	26
Steller's Jay	0.16	0.43	0.72	0.48	27	0.47	0.31	-0.38	0.71	29
Mountain Chickadee	0.96	0.75	-0.48	0.64	35	0.71	0.31	-0.76	0.45	43
Red-breasted Nuthatch	1.61	1.15	-1.72	0.10	27	1.51	1.30	-0.49	0.63	31
Brown Creeper	0.69	0.40	-1.30	0.20	29	-0.29	0.17	1.81	0.08	34
Golden-crowned Kinglet	0.39	0.55	0.47	0.64	31	0.47	0.53	0.18	0.86	36
Hermit Thrush	0.75	0.18	-1.76	0.09	30	0.16	0.84	2.25	0.03	28
American Robin	-0.16	-0.28	-0.41	0.69	26	0.51	0.80	0.92	0.36	27
Yellow-rumped Warbler	2.31	2.38	0.12	0.91	30	1.88	1.19	-1.15	0.26	32
Western Tanager	0.43	0.25	-0.62	0.54	28	0.71	0.80	0.29	0.78	28
Fox Sparrow	0.04	-0.03	-0.30	0.77	20	0.75	0.29	-1.57	0.13	23
Dark-eyed Junco	0.67	0.27	-0.71	0.48	40	0.00	-0.07	-0.14	0.89	45
Cassin's Finch	0.75	0.50	-0.75	0.46	42	-0.43	-0.19	0.77	0.45	39
Pine Siskin	0.71	0.82	0.41	0.69	35	0.04	0.36	0.75	0.46	26

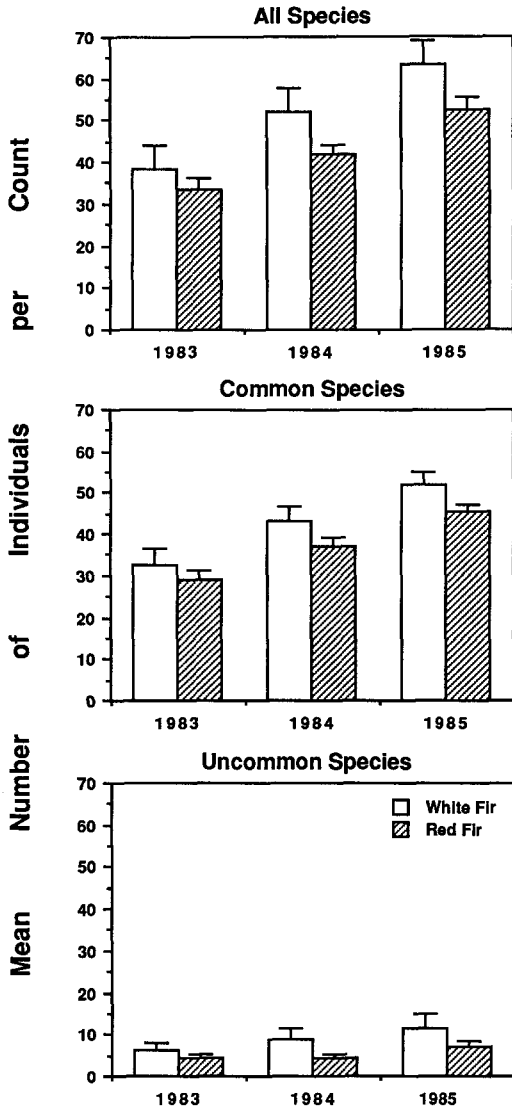


FIGURE 3. Abundances of all species, common species, and uncommon species in each habitat and year. Lines on histograms indicate the upper bounds of the 95% confidence intervals for each mean abundance. Comparisons of the confidence intervals within one habitat type are valid, whereas they are not valid between habitat types because of the difference in sample sizes.

Mountain Chickadees, Yellow-rumped Warblers, Cassin's Finches, and Pine Siskins were more abundant in red fir (Table 6). Hermit Thrush numbers fluctuated between the two habitat types.

ATC and the abundances of common species pooled increased linearly within both white and red fir ($F = 219.82$; $df = 1, 32$; $P < 0.0001$ for

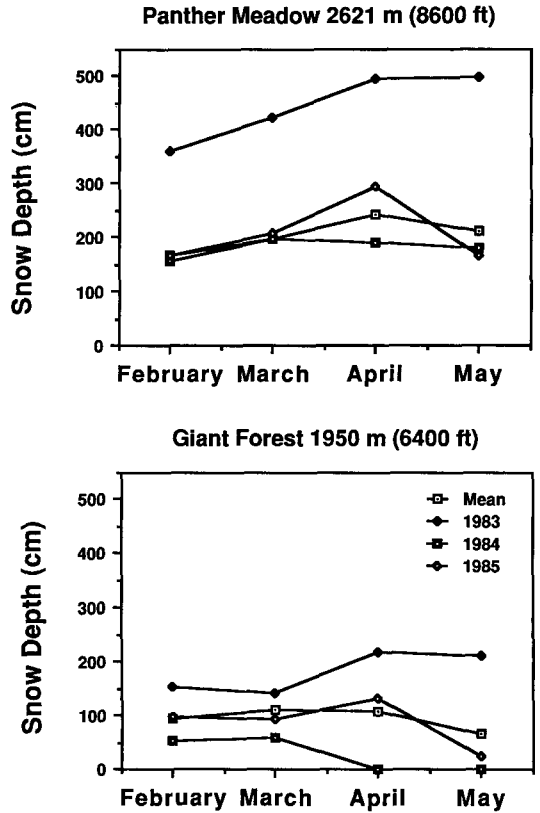


FIGURE 4. Snow-depth records for 1983, 1984, and 1985, and long-term averages (monthly n ranged from 45 to 56 years for Giant Forest and from 47 to 61 years for Panther Meadow) from two representative snow-survey locations.

total abundances in white fir; $F = 213.06$; $df = 1, 66$; $P < 0.0001$ for total abundances in red fir; $F = 165.65$; $df = 1, 32$; $P < 0.0001$ for common species in white fir; and $F = 228.34$; $df = 1, 66$; $P < 0.0001$ for common species in red fir) (Fig. 3). The mean abundance of uncommon species pooled also increased linearly in white fir ($F = 27.30$; $df = 1, 32$; $P < 0.0001$) and red fir ($F = 51.62$; $df = 1, 66$; $P < 0.0001$). However, the greatest increase of uncommon species in red fir occurred in 1985 (Fig. 3).

SNOW ACCUMULATION

The winter 1982-1983, an El Niño winter, was the most extreme on record, both in the amount of snow that fell (see Hejl and Beedy 1986) and in the amount that lasted well into the summer. Snow accumulation reflected both snowfall and melt patterns. Mean snow depth (calculated from 41- to 61-year averages; some data were missing,

TABLE 8. Arthropod biomass (g) in late summer from conifer foliage on six study sites indicating differences according to elevation and year. Type abbreviations: WF = sites dominated by white fir; RF = sites dominated by red fir.

Site	Type	Elevation (m)	1983	1984	1985	Mean biomass/site
178	RF	2,512	0.0068	0.0046	0.0517	0.0210
128	WF	2,438	0.0079	0.0105	0.1398	0.0527
330	RF	2,268	0.0119	0.0243	0.1029	0.0464
407	RF	2,195	0.0168	0.0174	0.0445	0.0262
331	RF	2,121	0.0032	0.0238	0.0764	0.0345
415	WF	2,024	0.0426	0.0740	0.2053	0.1073
Mean biomass/year			0.0149	0.0258	0.1034	

especially for early years) increases with elevation. Giant Forest, located approximately 60 m lower than our white fir sites, averages about half the snowpack of Panther Meadow, located 671 m higher, fairly directly upslope, and in the midst of some of our red fir sites (Fig. 4). Greater snow accumulation was recorded at all six sites in May 1983 than in any other year on record. Ignoring Nellie Lake data, which included many missing values for May, at least four of the five stations had snow-depth records exceeding one standard deviation above the mean during 1952, 1958, 1967, 1969, 1975, 1978, and 1983, or, on average, every 5 years. Many records were missing before 1952; however, none of the May records before 1952 included snow depths as great as those observed in 1983.

ARTHROPOD BIOMASS

In general, insect and spider biomass increased from 1983 to 1985 and from upper to lower elevations according to late summer biomass estimates (Table 8). The annual increase in arthropod biomass was much clearer than the elevational trend. The pattern of decreasing biomass with increasing elevation occurred in 1983 with one anomalous site. Annual and elevational differences from early summer samples paralleled those of late summer. Biomass did not noticeably differ between white and red fir trees on the same site. However, on the sites for which we had within-season samples, arthropod biomass was always greater in late summer than in early summer in 1984 and 1985. In 1983, the low insect and spider numbers showed no seasonal pattern.

DISCUSSION

We do not know what factor(s) resulted in low bird numbers on our sites in 1983. DeSante (1985)

found about half the total number of breeding territories in 1983, compared to 1981 and 1985, in a study on a 1-km² plot in eastern Sierra Nevada subalpine forest. He believes that immigration and emigration were the variables most affected. DeSante monitored fecundity and adult mortality, neither of which changed appreciably during any of the years of his study (1979 to 1985). Assuming that fecundity and adult mortality were similarly unaffected in our true fir stands, numbers could have been depressed in 1983 because of high winter mortality of young birds. Alternatively, birds may have moved downslope to breed, as we know that many of these bird species regularly breed over a wide elevational range (Verner and Boss 1980, Beedy 1982) and are found at elevations below white fir forests and above red fir forests. Beedy (1982) and Granholm (1982) recorded similar depressions of resident bird numbers following the harsh winter of 1978 in the western Sierra Nevada, but their counts of migrants showed no definite pattern. However, they did not study these areas in 1979 so would have missed a rebound in resident bird numbers, if it occurred.

Increases in BSR and individual species' abundances, irrespective of migratory status, could have resulted either from low winter mortality of young birds and/or from birds moving upslope to breed in suitable habitat. Based on DeSante's (1985) findings that neither fecundity nor adult mortality were affected by the heavy winter of 1983, we suggest that survival and recruitment of young birds into the breeding population are the factors most affected by severe winter snows.

Our patterns of immigration and emigration may be evidence of a "source-sink" structuring of populations (Wiens and Rotenberry 1981) in montane communities. Abundances of common species were similar in both habitats in 1983 and

increased linearly in both habitats in 1984 and 1985 with numbers always greater in white fir. BSR and abundances of the uncommon species were similarly low in white fir and red fir sites in 1983, increased only in lower-elevation white fir in 1984, and increased in both white and red fir in 1985. We suggest that optimal habitats of many of these species, especially uncommon ones, occur at lower elevations and that these areas harbor "source" populations. Individuals unable to find breeding territories at lower elevations move upslope into less suitable, or "sink," habitats during crowded years. Morrison et al. (1987) documented decreasing bird numbers from 1983 to 1985 in a mixed-coniferous forest, the vegetation type which borders the lower elevation limit of white fir forests. Some of the "surplus" birds on their sites in 1983 may have moved to higher elevations in 1984 and 1985. However, observer error could have caused up to 25% lower counts in 1985 in Morrison et al.'s data set (one of their two observers in 1985 showed 25% lower counts than the highest observer in a separate test of bird-counting ability; unpubl. observ., JV). It is likely that philopatric migrants return each year and many permanent residents often remain even in less suitable sink habitats, so some individuals are always present. "Permanent" residents may vary in elevation more than their name implies. For example, one pair of alpine-breeding Rosy Finches (*Leucosticte arctoa*) bred in the subalpine during summer 1983 (DeSante 1985), evidence of a permanent resident moving downslope to breed.

Red fir often has snow present into June (Oosting and Billings 1943, Granholm 1982, snow-survey data), so we doubt that the absence of snow is used as a proximate cue for habitat selection by all birds. Recent data (unpubl. observ., SJH) suggest that short-distance migrants move into red fir sites in April in spite of 90% snow cover to depths of 1 to 2 m. Therefore, snow presence is not likely to keep short-distance migrants downslope even after a severe winter. The limited data on insect biomass lead us to suggest differences in insect density as cues for habitat selection. Young birds, both permanent residents and migrants, could move into an area, monitor insect abundance, and leave the area shortly thereafter if insect abundance were not satisfactory for breeding. Late spring and summer snows could also affect last-minute decisions about habitat selection. Beedy (pers. comm.) noted that

insectivorous birds abandoned one of his study sites after a late storm in the summer of 1977. Flying distance is short between habitat types at different elevations in the Sierra Nevada, so rapid adjustments in habitat distribution are likely to impose little energetic cost.

We believe that the richness and abundance of breeding birds in true fir forests of the Sierra Nevada regularly fluctuate, because the mean interval between large snow years in the central Sierra Nevada has been 5 years during the last 34 years. Furthermore, lower population numbers (number of species, total abundance, abundances of common and uncommon species) probably occur more often in red fir than in white fir, because red fir forests typically receive more snow each year, and have a more extreme climate in general.

Perhaps this phenomenon is typical of montane forests in the western United States. Szaro and Balda (1986) recorded lower bird numbers and species richness in ponderosa pine forests in northern Arizona in the summer following the heaviest snowfall on record. Noncavity nesters, summer residents, and permanent residents were negatively correlated with precipitation, but cavity nesters were not. Bock and Lynch (1970) studied birds in a jeffrey pine (*Pinus jeffreyi*)-white fir forest in the eastern Sierra Nevada. Only seven of 32 species had higher densities in 1967, following a year with high snowfall. Six of the seven were migrants.

We cannot totally discount the effect of improved bird-identification skills of the primary observer in this study. However, it is unlikely that abundances of the common species would have been affected by observer improvement during the years of the study, because the calls and songs of those species were well known before the study began. Although BSR values could have been affected by improved ability to detect rare species, it is unlikely that this effect would have differed between white and red fir sites.

Based on the results of this and other studies in the Sierra Nevada, we suggest that alternating increases and decreases in bird numbers in these habitats are not unusual phenomena. However, Weatherhead (1986) has cautioned about the interpretation of "unusual" events and we do not want to misinterpret our data. We agree with Weatherhead that a long-term study such as that of Holmes et al. (1986) would enable us to set these numbers in better perspective.

Furthermore, data from a subset of individual sites would not necessarily lead to the same conclusions. For example, if we had examined only sites 333 and 407, we would have decided that BSR declined between 1983 and 1985, a conclusion which is diametrically opposed to that reached here. On the other hand, Beedy (1982), Granholm (1982), and Bock and Lynch (1970) all found population declines in most resident species following severe winters, in spite of the fact that they all had few study sites. This fact further substantiates our conclusion that excessive snowfalls typically, and on a broad scale, lower the richness and abundance of birds breeding in true fir forests of the Sierra Nevada.

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