Habitat Association Patterns of Breeding Birds and Small Mammals in Douglas-Fir/Hardwood Stands in Northwestern California and Southwestern Oregon

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Abstract

We surveyed birds and small mammals in 45 forest stands from southern Oregon, near Cave Junction, south into northern California, near Branscomb. Over this 350-km distance, we found 71 species of birds and 7 species of mammals that were common enough for detailed analysis. Fourteen species of birds and two mammals reached peak abundances in older (mature and old-growth) forests; however, none appeared limited to these forests. The species were: Allen's hummingbird, hairy woodpecker, pileated woodpecker, Hammond's flycatcher, western flycatcher, gray jay, chestnut-backed chickadee, red-breasted nuthatch, brown creeper, winter wren, golden-crowned kinglet, wrentit, hermit warbler, black-headed grosbeak, Douglas' squirrel, and the California red-backed vole. In addition, about half of the species were correlated with total conifer or hardwood stems. The abundance of many species also differed among the three geographic regions we sampled. These differences could also be associated with elevation because our northern stands tended to be at higher elevations than were the southern stands. Our community analysis of the birds showed separations between different regions, and between the avian communities of young forests and those of older (mature and old-growth) forests. The mature and old-growth bird communities were not readily separable from each other.

Introduction

The Douglas-fir forests of northwestern California are a major source of timber products in the United States, with almost half of the Nation's timber supply contained in the old-growth forests of the West (Society of American Foresters Task Force 1983: 1). Clearcutting has been the primary method of harvesting timber in the region for the past 30 years. Morrison (1988) has documented the great reduction of old-growth timber in many forests of the Pacific Northwest, which includes Washington, Oregon, and northern California.

Present management guidelines state that the USDA Forest Service shall "maintain viable populations" of all vertebrates found on each National Forest (National Forest Management Act 1976, 16 U.S.C. 1600-1614), yet the impacts of the decline of old-growth forests on vertebrate populations in northwestern California are uncertain, with only a few studies on the subject (Hagar 1960, Raphael 1984, Raphael and others 1988). Our study's goal is better understanding of the association patterns of flora and fauna across a chronosequence of forests in the Northwest; it was conducted as a part of research that extends north into Washington (Carey and Spies, this volume; Ruggiero and Carey 1984).

We studied the relative abundance of small mammals and diurnal birds along an age gradient of selected forest stands in northwestern California and southwestern Oregon during the summers of 1984 and 1985. We surveyed the entire diurnal avian community and trapped small mammals to determine if the relative abundance of each species differed between the stands, and to determine which habitat variables correlated with the abundances of each species. We detected 23 small mammal species and 102 bird species over 2 years of field work; in this paper, we concentrate on the more common species.

Methods

Study Areas

We selected 45 principal study stands (table 1) in three regions of northwestern California and southwestern Oregon to represent a successional gradient typical of the Douglas-fir communities (see frontispiece). We selected stands nonrandomly based on accessibility by road, presence of a representative age-class of trees, and moderate topography. The stands were conveniently divided into three geographical regions of 15 stands each (table 1): Cave Junction in the north, Willow Creek in the central area, and Branscomb in the south. Stands ranged in elevation from about 400 m to 1550 m, and most were dominated by Douglas-fir in association with tanoak and madrone. Six low-elevation plots had some redwood, and four high-elevation stands in the Cave Junction region were dominated by white fir.

Bird Counting Techniques

Diurnal birds were counted in 1984 and 1985 during the breeding seasons from May to June. Each stand was visited 5 to 7 times each field season, with counts conducted over the entire breeding season at the rate of about once per week for each stand. We minimized observer bias by rotating observers at each stand. In 1984, we had 5 to 6 observers per region, so each stand was usually counted once per observer. During the 1985 field season, we had only 3 to 4 observers in each region, so stands were usually visited on the average of twice per observer. Counts were conducted on 12 fixed stations placed 150 m apart at least 100 m from adjoining habitat types. Observers counted at each station for 8 minutes, recording horizontal distance to each bird seen or heard. All counts were initiated within 15 minutes of official sunrise and took approximately 3.5 hours to complete, to minimize time-of-day bias.

We used the number of individuals detected per station as a relative index of population abundance, which corrects for differences in effort. We did not establish an arbitrary distance from the observer beyond which detection would be excluded because the unit of analysis was the stand as a whole, not individual stations within the stand. Double registrations of an individual consequently would not affect the conclusions. We include in this report only those species that we recorded more than about 10 times during the survey in abundances greater than or equal to a total of 0.001 birds per station, which included all but the rarest species.

Mammal Trapping

For the mammal studies, we included an additional two stands at Butte Creek, near Dinsmore, California. A single trapping-grid for snap and livetrapping was laid out in each stand in a pattern of 12 rows with 12 trap stations per row. Trap stations were placed at 15-m intervals in a 165-m x 165-m grid.

In 1984, two Museum Special snaptraps were placed at each trap station within 1.5 m of the grid coordinate in all 47 stands. We trapped in six stands simultaneously (two in each region) for 5 days (4 nights) until all stands were sampled (July 3 to August 31). In 1985, a single Sherman livetrap (7.6 cm x 8.9 cm x 22.0 cm) was used at the same stations in 43 of the stands, and we trapped again in six stands during each 5-day session from July 9 to August 30. We did not livetrap in four stands (two in Branscomb area and two in Cave Junction area). We also used pitfall traps to sample small mammal populations in all 47 stands during both 1984 and 1985. A pitfall- grid consisted of six rows of six pitfall traps per row spaced at 15-m intervals in each stand. Snap and pitfall grids were usually separated by more than 100 m. Traps were constructed from two No. 10 cans taped together and sunk until the top was flush with the ground. A funnel collar prevented animals from escaping. We propped a cedar shake 3 to 4 cm above the opening of each pitfall trap to act as a cover, and examined the traps at 5-day intervals for 50 days in October and November 1984, and for 30 days in October 1985. In the analyses below, we used the number of mammals captured, without standardizing the data for effort (table 4). Total trap nights were adjusted for inoperative traps.

Table 1--List of study stands by region, with stand abbreviation, elevation, mean age, age-class, and mean density in stems per 1000 m^2 of hardwood and conifer trees

Region	Stand	Elevation	Canopy trees		Mean density of trees	
			Age	Age-class	Hardwoods	Conifers
Cave Junction						
(AC)	Althouse Flat	427	107	Mature	0.531	1.890
(BP)	Buck Peak	1366	60	Young	.034	.919
(CG)	California Gray Back	1556	265	Old	.000	1.32
(FR)	Frog Pond	1439	196	Mature	.000	3.141
(GG)	Galagy Grove	1334	259	Old	.000	2.639
(HC)	Happy Camp Road	1053	179	Mature	.179	1.89
(HO)	Holcomb Peak	1411	235	Old	.042	3.235
(LG)	Little Grayback	1205	72	Young	.016	1.39
(LH)	Left Hand	1362	96	Young	.044	2.997
(OC)	Oregon Caves Road	872	192	Mature	.316	1.17
(PM)	Page Mountain	1519	204	Old	.007	3.450
(SK)	Skag Hope	1305	267	Old	.011	3.890
(TU)	Tunnel Site	624	65	Young	.368	1.679
(UH)	Upper Horse	1502	91	Young	.013	1.581
(WC)	Waters Creek	614	240	Old	.246	1.338
Willow Creek						
(BA)	Bald Mountain East	846	43	Young	.862	0.701
(BE)	Brannon Mountain	750	236	Old	.597	1.379
(BM)	Beartooth Mountain	1144	327	Old	.383	2.176
(BR)	Brush Mountain	1050	116	Mature	.420	1.773
(CC)	Cedar Creek	665	347	Old	.396	1.728
(EB)	East Fork Big Creek	1134	246	Old	.589	1.383
(FN)	Fawn Prairie	750	44	Young	.983	.945
(GR)	Gray II	972	101	Mature	.292	1.481
(HP)	Hennessy Peak	949	100	Mature	.172	1.700
(LE)	Lord Ellis	778	48	Young	1.366	1.024
(LR)	Ladder Rock	805	319	Old	.828	2.072
(SF)	South Fork	659	289	Old	.470	1.291
(SH)	Sharber	747	283	Old	.673	.932
(TT)	Tish Tang	680	204	Old	.888	1.484
(WR)	Waterman Ridge West	633	85	Mature	1.091	1.140
Branscomb						
(AP)	Alpine	444	210	Old	.730	1.899
(BT)	Barnes	467	53	Young	.357	.32 9
(DP)	Darby	587	240	Old	.317	1.021
(EC)	Elder Creek	555	155	Mature	.402	2.361
(EH)	Elkhorn Ridge Hydric	518	137	Old	.230	.603
(EX)	Elkhorn Ridge Xeric	518	140	Mature	.487	.291
(FC)	Fox Creek	543	187	Old	.576	1.757
(FP)	Fanny's Place	445	122	Mature	.375	1.372
(HN)	Harwood's Ninty	695	118	Mature	1.010	.424
(HT)	Homestead	726	40	Young	1.071	1.300
(MS)	Mud Springs	689	70	Young	.691	.678
(SC)	Skunk Creek	529	291	Old	.278	1.223
(SG)	Standley Grove	481	450	Old	.082	3.555
(TM)	Ten Mile	445	241	Old	.317	1.718
(WH)	White House	427	136	Mature	.655	1.451

Vegetation Sampling

Vegetation was quantified on each of the 12 bird-count stations in each stand. On the snap-livetrap grid we measured 16 plots overlaying the 144 trap stations. Nine vegetation plots were also uniformly distributed among the 36 pitfall stations. For this analysis, we used the mean number of all hardwood and conifer stems greater than 50 cm in d.b.h. within 15 m of each mammal-trapping station and 25 m for bird observations. We reasoned that, for this study, individual plant species would be too detailed for our analysis.

Stand ages were based on data supplied by B. Bingham (pers. comm.) from core samples of three to five dominant Douglas-firs on each of three plots in each young and mature stand (up to about 180 years). In old-growth stands, tree cores could not always be taken because trees were so large and had rotten cores; thus, some stand ages were estimated from rings counted on stumps in adjacent clearcuts or beside nearby roads, or they were based on ages provided by local Forest Service offices.

We minimized the number of variables for the small mammal community by comparing the capture rates associated with logs that have fallen relatively recently, hard logs of decay-classes 1 and 2 of Thomas (1979: 80), and soft logs of decay classes 3 to 5.

Data Analysis

The objective of this analysis was to estimate how much variation in bird abundance among stands could be explained by stand age or geographical region, and whether abundance was affected by interaction between stand age and region. For most analyses, stand age was considered as a continuous variable, and entered into calculations as a square-root transformation. Region was considered a categorical variable. A probability level of $P < 0.05$ was used to signify statistical significance.

We considered that the bird counts, as discrete variables, approximated normal distributions with means linear on the independent variables and with equal variances.

A general linear model (GLM) in SAS (Freund and others 1986: 145) was used to compare relations between the abundance of each bird species with stand age and region. This comparison was treated as an analysis of covariance with interaction between age and region, with region as the covariate. The interaction term determines if the relation (the slope of the line describing the relation between age and abundance) was statistically different among regions.

The SAS procedure "GLM," produces two sets of statistics, Type I and III Sums of Squares, which we used in constructing table 2. If the interaction between age and region was not significant, then we used the statistics from Type I (the unadjusted treatment sums of squares), where age was entered into the model after region. If the interaction term was significant, then we used Type III (adjusted treatment sum of squares), which takes into account the other variables before calculating the effect of the variable under consideration. For example, if an age and region interaction was significant, then the statistic appearing in table 2 was the effect of age after accounting for the effects of both region and the interaction of age and region.

We also treated stand age as a classification variable when separating the sites into young, mature, or old-growth, based on a discriminant function analysis of vegetation data sampled from the entire stand (Bingham and Sawyer, this volume). These classifications, based on vegetative structure and composition, sometimes differed from stand age as determined by counting tree rings. Bird abundances are presented in table 2 according to the stand-age classifications of Bingham and Sawyer. A least-squares test (Freund and others 1986) determined significant differences in bird abundances between age-classes and regions.

We compared numbers of species and individuals detected between years and habitat types by using Pearson product-moment correlation coefficients.

Our analysis of the data aggregated the various stands according to similarities in the abundance of bird species found in each stand. For this, we used Ward's method of cluster analysis (SAS 1982: 423), but only for the commoner species, which we defined as the 29 species with average abundances greater than 0.1 birds per station in either 1984 or 1985 (table 3). We acknowledge that this analysis is only an approximation because it is not based on actual densities, but we believe that the figures were indicative of the relative abundance of most species.

Table 2-Comparison of the number of individuals of each bird or mammal species detected or captured per station in the three regions; the significance (*P* <) of region alone as a contribution to a model; the number of individuals per station in young, mature, and old-growth stands; the significance of age alone as a contribution to a model; the significance of the interaction of age and region; and the amount of variance explained by the model (R^2)

Species		Region: Brans-comb	Region: Willow Creek	Region: Cave Junction	Region signif-icance	Age of stands: Young	Age of stands: Mature	Age of stands: Old-growth	Age signif-icance	Age*Region signif icance	R^2
Turkey vulture		0.008	0.001	0.000	0.0369	0.000	0.003	0.005	0.3124	0.5512	0.1951
Northern goshawk		.001	.003	.001	.4094	.000	.001	.003	.1561	.7576	.1030
Red-shouldered hawk		.006	.000	.000	.3800	.000	.000	.005	.4709	.5607	.0864
Red-tailed hawk		.004	.006	.008	.7967	.001	.009	.006	.2979	9966	.0389
Blue grouse		.000	.000	.051	.0001	.033	.002	.021	.9224	.9369	.3848
California quail		.014	.001	.009	.3832	.027	.004	.001	.0128	.4107	.2137
Mountain quail		.325	.075	.071	.0001	.116	.169	.169	.9229	.9037	.3844
Band-tailed pigeon		.002	.013	.003	.0606	.015	.001	.005	.2360	.9301	.1635
Mourning dove		.019	.001	.025	.4213	.013	.024	.008	.4902	.6863	.0717
Flammulated owl		.000	.001	.003	.0932	.000	.002	.002	.1831	.3008	.1936
Northern pygmy-owl		.030	.257	.005	.0828	.005	.025	.024	.2228	.3939	.1834
Anna's hummingbird		.011	.003	.003	.0262	.004	.005	.007	.1425	.0036	.3402
Allen's hummingbird	+	.046	.002	.006	.0013	.003	.007	.036	.0008	.0001	.5540
Acorn woodpecker		.075	.066	.066	.9853	.030	.093	.069	.9610	.4755	.0381
Red-breasted sapsucker		.025	.031	.030	.9042	.020	.031	.032	.6857	.1850	.0908
Downy woodpecker	-	.003	.001	.002	.1922	.001	.002	.002	.8319	.8798	.0876
Hairy woodpecker	-	.055	.048	.054	.8133	.034	.036	.076	.0133	.2767	.2007
White-headed woodpecker		.000	.001	.003	.2019	.000	.000	.003	.0562	.0900	.2403
Northern flicker		.426	.193	.159	.0001	.230	.253	.280	.2669	.3135	.5251
Pileated woodpecker	-	.152	.110	.089	.0880	.051	.127	.144	.0285	.9227	.2124
Olive-sided flycatcher	+	.016	.038	.119	.0003	.063	.025	.082	.0890	.5924	.3788
Western wood-pewee		.078	.009	.082	.0259	.044	.064	.056	.2404	.4916	.2185
Hammond's flycatcher		.000	.104	.374	.0001	.091	.157	.198	.0377	.2185	.4611
Dusky flycatcher		.000	.005	.053	.0001	.042	.008	.016	.2122	.2818	.4594
Western flycatcher	+	1.780	1.175	.520	.4531	.543	1.230	1.420	.0001	.0480	.8194
Ash-throated flycatcher		.015	.000	.000	.2297	.019	.002	.000	.1010	.0752	.2264
Gray jay		.000	.000	.011	.2236	.003-	.000	.007	.0360	.0257	.3881
Steller's jay		.978	.748	.555	.0007	.651	.850	.743	.8193	.8286	.3187
Scrub jay		.011	.004	.000	.0116	.010	.005	.002	.0772	.5351	.2720
American crow		.000	.001	.006	.1604	.001	.005	.000	.3631	.3815	.1459
Common raven		.373	.086	.083	.0001	.075	.213	.209	.3174	.4458	.5036
Mountain chickadee		.000	.000	.041	.0031	.016	.002	.022	.3456	.1819	.3149
Chestnut-backed chickadee	+	.609	.548	.317	.0001	.339	.533	.535	.0113	.9390	.5574
Bushtit		.013	.008	.001	.1262	.005	.010	.006	.7712	.0667	.2083
Red-breasted nuthatch		.264	.544	.830	.0001	.335	.514	.684	.0047	.1853	.5344
White-breasted nuthatch		.000	.014	.002	.1906	.001	.010	.004	.7786	.9520	.0854
Brown creeper	-	.528	.218	.222	.0001	.118	.313	.438	.0001	.0001	.8521
Bewick's wren		.001	.000	.004	.0783	.004	.001	.001	.1569	.2103	.2164
House wren		.000	.005	.005	.4594	.005	.005	.002	.3365	.7833	.0720
Winter wren		.084	.160	.235	.0452	.173	.068	.229	.0134	.0319	.3381
Golden-crowned kinglet	+	.013	.270	774	.2346	.417	.242	.411	.1560	.0301	.6618
Townsend's solitaire		.003	.050	.149	.0018	.139	.034	.057	.0710	.0291	.4630
Hermit thrush	+	.382	.671	.453	.0413	.551	.422	.543	.9865	.9476	.1528
Swainson's thrush		.000	.023	.008	.1541	.016	.001	.016	.8395	.7464	.1046
American robin	-	.251	.086	.124	.0024	.053	.195	.173	.1515	.2447	.3293

Table 2-continued

Species		Region: Brans-comb	Willow Creek	Cave Junction	Region signif-icance	Age of stands: Young	Mature	Old-growth	Age signif-icance	Age*Region signif icance	R^2
Varied thrush		0.000	0.057	0.008	0.0132	0.081	0.001	0.008	0.1871	0.0413	0.2756
Wrentit	+	.222	.085	.009	.0118	.054	.079	.155	.0063	.1002	.3728
Solitary vireo	-	.462	.306	.148	.0078	.110	.453	.284	.9630	.6651	.2331
Hutton's vireo	-	.186	.126	.045	.0005	.123	.137	.102	.0931	.3535	.3776
Warbling vireo	+	.781	.291	.147	.0001	.359	.582	.283	.0090	.0001	.6070
Orange-crowned warbler		.109	.011	.000	.0010	.073	.029	.032	.2956	.6806	.3204
Nashville warbler	-	.144	.148	.495	.0021	.306	.280	.224	.3731	.3871	.3060
Yellow-romped warbler		.001	.037	.321	.0001	.155	.062	.150	.5975	.3089	.4645
Black-th. gray warbler	-	.772	.220	.357	.0030	.484	.632	.279	.0200	.0036	.4468
Townsend's warbler	-	.000	.003	.021	.0001	.011	.008	.006	.5187	.6717	.4841
Hermit warbler	+	1.306	2.279	1.695	.0032	1.155	1.761	2.078	.0040	.0247	.4630
MacGillivray's warbler	+	.000	.009	.033	.0001	.027	.010	.011	.0880	.0964	.5076
Wilson's warbler	+	.550	.205	.022	.0001	.165	.259	.309	.0466	.1203	.5021
Western tanager	-	1.089	:677	.367	.0002	.319	.933	.730	.4929	.2290	.3833
Black-headed grosbeak	-	.537	.583	.242	.0414	.204	.552	.503	.8691	.0235	.3260
Lazuli bunting		.000	.005	.000	.0095	.001	.002	.003	.3790	.8622	.2295
Rufous-sided towhee	-	.350	.007	.009	.0001	.097	.156	.106	.5147	,3277	.6540
Fox sparrow		.000	.000	.013	.0119	.005	.001	.008	.4914	.3890	.2407
Song sparrow		.000	.016	.001	.1153	.017	.002	.003	.1152	.1683	.1998
Dark-eyed junco	-	.490	.374	.600	.1137	.401	.554	.478	.9428	.0791	.2045
Brown-headed cowbird		.001	.006	.040	.0473	.010	.034	.004	.4290	.5470	.1784
Purple finch		.043	.097	.099	.0966	.052	.084	.091	.2313	.2122	.1987
Red crossbill		.011	.015	.031	.0728	.026	.013	.021	.5273	.0249	.2474
Pine siskin		.004	.075	.395	.0001	.164	.127	.182	.0802	.1588	.7240
Lesser goldfinch		.004	.001	.006	.2265	.004	.004	.003	.9962	.8748	.0792
Evening grosbeak		.000	.002	.053	.0001	.031	.012	.017	.4127	.8730	.6541
Chipmunks		.007	.007	.035	.0003	.020	.016	.014	.9837	.9731	.3408
Douglas' squirrel		.072	.315	.443	.0001	.180	.235	.362	.0363	.0755	.4589
Western gray squirrel		.050	.007	.030	.0004	.017	.037	.028	.9808	.8263	.3340

Note: When a significant difference was found between the abundance of a species by age-classes or regions, those that were statistically indistinguishable by a least-squares test are joined by an underline. For nonadjacent, indistinguishable column values (for example, young and old-growth) the underline is disjunct. If all three differ significantly from each other, each is underlined. A plus (+) or minus (-) after the species' name indicates a significantly positive or negative relation to stand age according to the analysis of Raphael (1984).

Results

Bird Abundances

Overall abundance patterns-Seventy-one bird species (table 3) were found in the study plots in both years in numbers greater than 0.001 birds per station. The most abundant species was the hermit warbler, with over 1.7 birds per station in both years. The western flycatcher was next in abundance with more than 1.1 birds per station.

Some birds began to reach the limit of their distributions within the geographic range of this study. For instance, blue grouse and gray jay were only found at Cave Junction in the north, and Hammond's flycatcher was not found at Branscomb in the south. These species could be found in areas we did not count to the north or south, but in limited numbers. They also probably were largely limited by the attitudinal gradient between study stands. The Cave Junction stands were generally at higher elevations and Branscomb tended to be lower.

We divided the species into three groups: year-round residents, short-distance migrants (birds wintering in the United States), and long-distance migrants. More than half (59 percent) of the species were residents, 11 percent were short-, and 30 percent long-distance migrants. By contrast, only 42 percent of individuals (birds per station) were residents, 6 percent short, and the majority (52 percent) long-distance migrants.

Comparison between years-We compared, by correlation, the abundance of each species between years in each stand to determine the concordance of the 2 years' data. The closer the agreement between the 2 years, the greater the likelihood (but, by no means, certainty) that some aspect of the habitat was important in determining the abundance of that species at any sampling point. The less the agreement, the greater the likelihood that stochastic events in the population could be responsible for the abundance of the species.

Table 3-Mean number of detections of each bird and mammal species per station in 1984 and 1985, the linear correlation (R^2) between years and its sign, and the linear correlation (R^2) between the number of detections and the abundance of hardwood and conifer trees and its sign (significant correlations are indicated as: * = $P \leq .05$, ** = $P \leq .01$, and *** = $P \leq .001$)

	Year				Tree type	
Species	1984	1985	R^2	P	Hardwood (R^2)	Conifer (R^2)
Turkey vulture	0.003	0.003	0.47	0.0011	0.01	-0.16
Northern goshawk	.001	.002	-.06	.7017	.03	.11
Red-shouldered hawk	.000	.004	.00	1.0000	-.05	-.11
Red-tailed hawk	.007	.006	-.06	.6836	-.17	-.23
Blue grouse	.020	.014	.37	.0122	-.52***	.27
California quail	.011	.006	.90	.0001	.24	-.24
Mountain quail	.160	.154	.68	.0001	.05	-.12
Band-tailed pigeon	.007	.005	.37	.0115	.29*	-.23
Mourning dove	.012	.018	.88	.0001	.03	-.03
Flammulated owl	.001	.001	-.06	.7208	-.24.	.40**
Northern pygmy-owl	.019	.022	.26	.0796	.04	-.29
Anna's hummingbird	.009	.003	-.10	.4978	.00	.19
Allen's hummingbird	.027	.009	.09	.0001	-.17	.32*
Acorn woodpecker	.055	.082	.88	.0001	.15	-.10
Red-breasted sapsucker	.023	.346	.65	.0001	-.31*	.10
Downy woodpecker	.001	.003	-.08	.5931	.07	.00
Hairy woodpecker	.061	.044	.24	.1112	-.29	.27
White-headed woodpecker	.001	.002	-.04	.8022	-.18	.26
Northern flicker	.269	.250	.63	.0001	.08	-.26
Pileated woodpecker	.136	.098	.71	.0001	-.03	-.10
Olive-sided flycatcher	.041	.074	.62	.0001	-.58***	.53***
Western wood-pewee	.045	.068	.63	.0001	-.29	.42**
Hammond's flycatcher	.154	.165	.92	.0001	-.44**	.46**
Dusky flycatcher	.015	.023	.55	.0001	-.48***	.20
Western flycatcher	1.138	1.177	.91	.0001	.17	-.12
Ash-throated flycatcher	.005	.005	.98	.0001	.00	-.26
Gray jay	.005	.003	.21	.1611	-.41**	.33*
Steller's jay	.791	.730	.61	.0001	.12	-.37*
Scrub jay	.005	.005	.21	.1639	.25	-.34*
American crow	.002	.002	.54	.0001	.01	.03
Common raven	.152	.209	.88	.0001	.08	-.21
Mountain chickadee	.014	.013	.76	.0001	-.41**	.13
Chestnut-backed chickadee	.501	.482	.52	.0003	.36*	-.20
Common bushtit	.011	.004	.05	.7498	.21	-.15
Red-breasted nuthatch	.492	.600	.89	.0001	-.51***	.53***
White-breasted nuthatch	.010	.001	.86	.0001	-.10	.00
Brown creeper	.337	.308	.93	.0001	-.19	.28
Bewick's wren	.001	.002	.36	.0144	-.21	.00
House wren	.001	.006	.13	.4139	-.25	.09
Winter wren	.194	.125	.74	.0001	-.33*	.54***
Golden-crowned kinglet	.374	.331	.91	.0001	-.56***	.60***
Townsend's solitaire	.057	.077	.70	.0001	-.52***	.22
Hermit thrush	.447	.557	.71	.0001	.40**	-.31*
Swainson's thrush	.013	.007	.15	.3250	.19	.11
American robin	.165	.143	.69	.0001	-.15	.06
Varied thrush	.020	.024	.67	.0001	.43**	-.12
Wrentit	.090	.121	.96	.0001	-.09	.06
Solitary vireo	.279	.331	.78	.0001	.23	-.19
Hutton's vireo	.109	.129	.65	.0001	.66***	-.50***
Warbling vireo	.447	.366	.91	.0001	.43**	-.28
Orange-crowned warbler	.040	.040	.88	.0001	.09	-.23

Table 3-continued

Species	Year: 1984	1985	R^2	P	Tree type: Hardwood (R^2)	Conifer (R^2)
Nashville warbler	0.236	0.288	0.85	0.0001	-0.27	-.09
Yellow-rumped warbler	.090	.149	.86	.0001	-.59***	.37*
Black-th. gray warbler	.354	.545	.84	.0001	.29	-.40**
Townsend's warbler	.003	.013	.20	.1873	-.36*	.31*
Hermit warbler	1.729	1.791	.86	.0001	-.22	.43**
MacGillivray's warbler	.011	.017	.37	.0199	-.40**	.15
Wilson's warbler	.206	.312	.94	.0001	.00	-.14
Western tanager	.702	.720	.84	.0001	.28	-.27
Black-headed grosbeak	.407	.501	.81	.0001	.40**	-.32*
Lazuli bunting	.003	.001	-.07	.6561	.18	-.07
Rufous-sided towhee	.081	.163	.94	.0001	.01	-.11
Fox sparrow	.001	.007	.50	.0005	-.37*	.17
Song sparrow	.008	.003	.95	.0001	.23	-.09
Dark-eyed junco	.509	.466	.88	.0001	-.44**	.22
Brown-headed cowbird	.021	.011	.80	.0001	-.10	.04
Purple finch	.068	.091	.31	.0359	-.11	.14
Red crossbill	.007	.031	.56	.0001	-.16	.09
Pine siskin	.162	.154	.83	.0001	-.63***	.42**
Lesser goldfinch	.003	.003	.55	.0001	-.09	-.05
Evening grosbeak	.018	.019	.81	.0001	-.48**	.39**
Chipmunks	.014	.019	.57	.0001	-.49***	.32***
Douglas' squirrel	.228	.325	.84	.0001	-.42***	.44***
Western gray squirrel	.031	.027	.60	.0001	-.02	.18

Although the majority of species had similar detection rates between years, 15 (21 percent) species showed significant differences (table 3). Most of these were rare species that undoubtedly varied because of the low numbers that were detected; only five were fairly abundant, having detection rates in either year in excess of 0.01 birds per station. Common species with abundances that changed significantly between years were the northern pygmy-owl, common bushtit, hairy woodpecker, Swainson's thrush, and Townsend's warbler. No common thread (such as food habits or foraging methods) unites these species; changes such as these are to be expected in a study of several species.

Geographic differences-Geographical variation in abundance is a pattern that overlies the species' response to changes in the amount and suitability of its habitat. Even though the habitat may be suitable, factors that are related to geography (such as climate or competition with existing species) may preclude or severely limit the species' presence, and mute its response to habitat.

By comparing the average number of species recorded on the 15 stands making up each region (fig. 1), we found that the northern Cave Junction stands averaged 37.3 species per stand, the Willow Creek stands averaged 32.4, and the Branscomb stands 32.6. The Cave Junction stands had significantly greater species richness than the southern stands (Duncan's Multiple Range Test).

We also found distinct patterns in the abundances of individual species in the northern and southern study sites. The majority of the species that showed differences between geographic regions were on a north-south cline (table 2). This cline was also of higher elevation with more true fir in the north, and more hardwoods in the south (table 1). When region was the only significant variable selected in a GLM model, 12 species were more abundant in northern stands, and 14„were more abundant in southern stands. Among the species more abundant in either the north or the south were species with geographic affinities in either direction. Significantly more common to the north were the more montane species, such as blue grouse, olive-sided flycatcher, dusky flycatcher, mountain chickadee, MacGillivray's warbler, Nashville warbler, yellow-rumped warbler, fox sparrow, pine siskin, and evening grosbeak. The brown-headed cowbird and Townsend's warbler were also more abundant in the northern regions. More abundant southern species included turkey vulture, mountain quail, Anna's hummingbird, northern flicker, Steller's jay, scrub jay, common raven, American robin, Hutton's vireo, solitary vireo, orange-crowned warbler, Wilson's warbler, western tanager, and rufous-sided towhee.

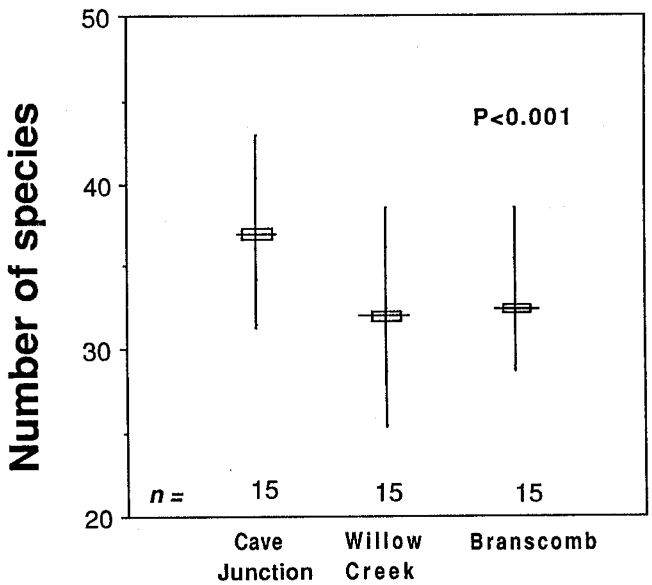

Figure 1-Comparison of the number of bird species by region. The means, standard errors, and ranges are shown for stands in each region. Sample size is shown below.

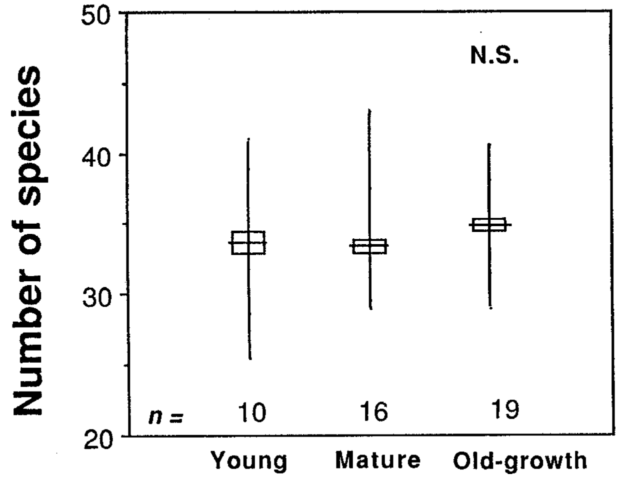

Figure 2-Comparison of the number of bird species by age-class. The means, standard errors, and ranges are shown for stands in each age-class. Sample size is shown below.

Few species showed other geographical patterns. Only two species were more abundant at the central Willow Creek stands: the lazuli bunting and hermit thrush. Only the western wood-pewee was less abundant in these central stands than in either the northern or southern stands.

Relation of abundance to stand age-By comparing the average number of species recorded in a stand by stand age (fig. 2), we found no difference among mature (33.5), young (33.7), and old-growth (34.7) forests (Duncan's Multiple Range Test). A correlation between stand age and average number of species also showed no relation ($r = 0.13$; $P = 0.132$), in contrast to results of Manuwal and Huff (1987), who found an increase in richness in their old-growth stands.

Stand age was an important factor in the abundance of many species in the community. For three species, the California quail, hairy woodpecker, and pileated woodpecker (fig. 3), age was selected as the sole significant contributor to our model (table 2). The quail was found in younger forests, and the two woodpeckers in greater numbers in older forests. When we used stand age as a classification variable in a separate analysis, three species (the hairy woodpecker, western flycatcher, and brown creeper) were significantly more abundant in old-growth forests than either the mature or young stands. Except for their occurrence in modest numbers in younger stands, these birds could be considered old-growth species.

For 17 species, or 24 percent of the 71 species total, both stand age and region were selected in the linear model as affecting the numbers of individuals recorded. The abundances of four species (chestnut-backed chickadee, Hammond's flycatcher, red-breasted nuthatch, and wrentit) were special in that they showed a consistent, positive relation with age among all three regions. That is, the interaction between age and abundance was not significantly different between regions. These species, along with the two woodpeckers mentioned above, showed the strongest affinity between abundance and age of forest.

Eight of the 17 species' abundances were positively related to stand age, and occurred most commonly in older forests: Allen's hummingbird, western flycatcher (fig. 3), gray jay, brown creeper (fig. 3), winter wren, golden-crowned kinglet, hermit warbler (fig. 3), and black-headed grosbeak. Only four species were more common in younger stands and also had their numbers influenced by region: Townsend's solitaire, varied thrush, warbling vireo, and black-throated gray warbler. The red crossbill was influenced by both region and stand age, but the effect of age was not clear. Although the abundances of many species were influenced by geography, these data showed that stand age was an important determinant for a large proportion of the species.

Selection of Forest Types

Comparing the stands as to their recorded number of species indicated that the richness of bird species was higher in stands with more conifers ($r = 0.28$; $P < 0.05$) and lower in

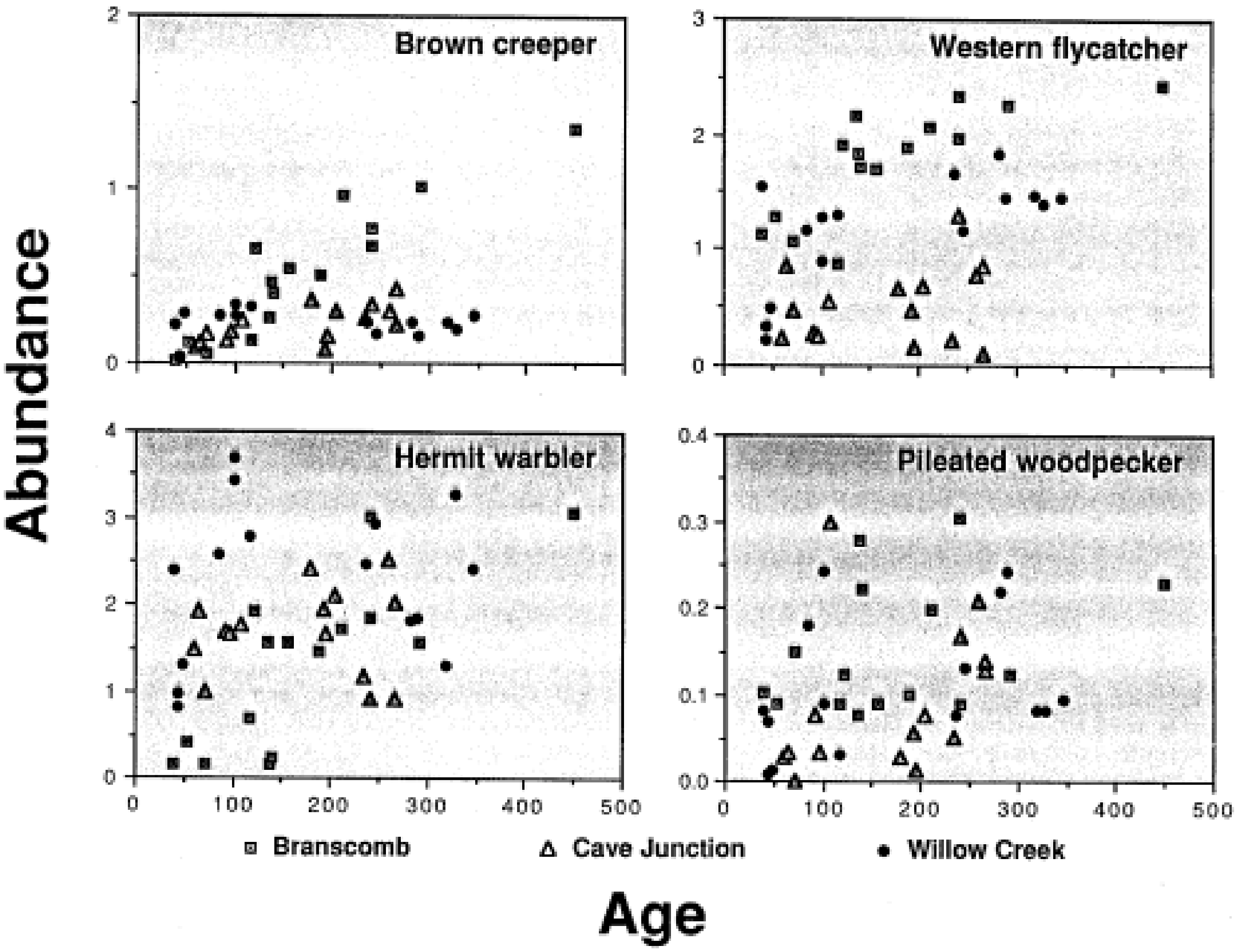

Figure 3-A comparison of the mean abundance of four bird species by stand and region with the square root of stand age as a continuous variable.

The abundance of many species was strongly correlated with the number of conifer or hardwood trees in the plots (table 3). In many of these species, we expected a positive correlation with one type and a negative with the other. Fourteen species were positively associated with conifers, which was the commonest association: flammulated owl, Allen's hummingbird, olive-sided flycatcher, western wood-pewee, Hammond's flycatcher, gray jay, red-breasted nut-hatch, winter wren, golden-crowned kinglet, yellow-rumped warbler, Townsend's warbler, hermit warbler, pine siskin, and evening grosbeak. Three species apparently had a negative association with conifers, but were not positively assoiated with hardwoods: Steller's jay, scrub jay, and black-throated gray warbler. Only seven species were positively associated with hardwoods: band-tailed pigeon, chestnut-backed chickadee, hermit thrush, varied thrush, Hutton's vireo, warbling vireo, and black-headed grosbeak. Finally, eight species were negatively correlated with hardwoods, but were not positively associated with conifers: blue grouse, red-breasted sapsucker, dusky flycatcher, mountain chickadee, Townsend's solitaire, MacGillivray's warbler, fox sparrow, and dark-eyed junco.

In all of these species, a more detailed, species-by-species analysis of habitat association patterns by plant species, as well as actual habitat use, is needed to determine the actual environmental factors that limit their distribution and abundance.

Table 4-Number of mammal captures by species and trapping technique within each study area[a] (for each technique, significant differences among captures in each study area are indicated by different letters after the totals)

	Technique								
	Pitfalls			Snap traps			Live traps		
Species	CJ	WC	BR	CJ	WC	BR	CJ	WC	BR
Trowbridge's shrew	349	296	247	146	124	84	27	57	17
Pacific shrew	14	16	3	19	40	5	6	2	3
Vagrant shrew	—	1	—	—	1	—	—	—	—
Marsh shrew	—	1	—	—	—	—	—	—	—
Shrew-mole	11	21	8	6	17	5	—	2	3
Coast mole	—	1	—	—	—	—	—	—	—
Chipmunks	2	—	—	25	3	1	171	39	72
Golden-mantled ground squirrel	—	—	—	—	—	—	1	—	—
Northern flying squirrel	6	—	—	—	1	—	2	5	1
Botta's pocket gopher	5	—	—	2	—	—	—	—	—
Deer mouse	51	36	27	72 A	212 B	209 B	41 A	204 B	159 B
Piñon mouse	1	7	8	25 A	67	113 B	113 A	76	124 B
Dusky-footed woodrat	—	2	—	1	—	3	4	6	18
Bushy-tailed woodrat	—	—	—	—	—	—	5	—	—
Western red-backed vole	341 A	186 A	45 B	73	49	35	28	32	41
Red tree vole	5	9	8	—	—	—	—	—	—
California vole	—	5	9	2	—	10	—	—	5
Long-tailed vole	2	—	—	—	—	—	—	—	—
Creeping vole	2	2	2	1	3	—	1	1	8
Black rat	1	—	—	—	—	—	—	—	—
Pacific jumping mouse	1	1	1	3	8	—	—	—	—
Ermine	—	—	—	—	—	—	5	—	1
Number of trap-nights[b]									
Cave Junction		43,200			19,275			7,263	
Willow Creek		48,960			18,559			8,289	
Branscomb		48,960			17,450			7,815	

[a] The three study areas are Cave Junction, Oregon (CJ), Willow Creek, California (WC), and Branscomb, California (BR).
[b] Totals were adjusted for traps damaged by bears.

Bird Community Organization

Using the number of individuals observed for each of the 29 most-common species as an approximation of the composition of the avian communities in a cluster analysis, we found some divisions (fig. 4). The divisions were largely geographical and probably depend on major vegetation types related to altitude. A secondary division occurred between the young stands and the combined group of mature and old-growth categories. No clear distinction could be made, judging from the bird community, between old-growth and mature communities.

The first division was a separation of the younger Branscomb stands, which contained a great deal of chapparal. The second division was between the upper elevation Cave Junction stands that had a substantial amount of true fir, and the young Willow Creek stands. The third major separation was between the Branscomb and Willow Creek stands with mature and old-growth being intermixed. The TU stand that Bingham (pers. comm.) classed as young did have some remnant old-growth trees, and the bird species associated with these trees apparently increased the stand's similarity to the older stands.

These patterns confirm the information from the individual species: that clear geographical separations are present, and that, although young forests differ from older forests, mature and old-growth forests are much alike.

Mammal Abundance Comparisons

Twenty-three species of small mammals were captured during the study, though several were represented by only a few individuals (table 4). The three techniques differed in their effectiveness for capturing different species of mammals. Six species or species groups had sufficient captures (≥_100 individuals or more, by one or more of the trapping techniques) to permit intensive analyses. These were the western

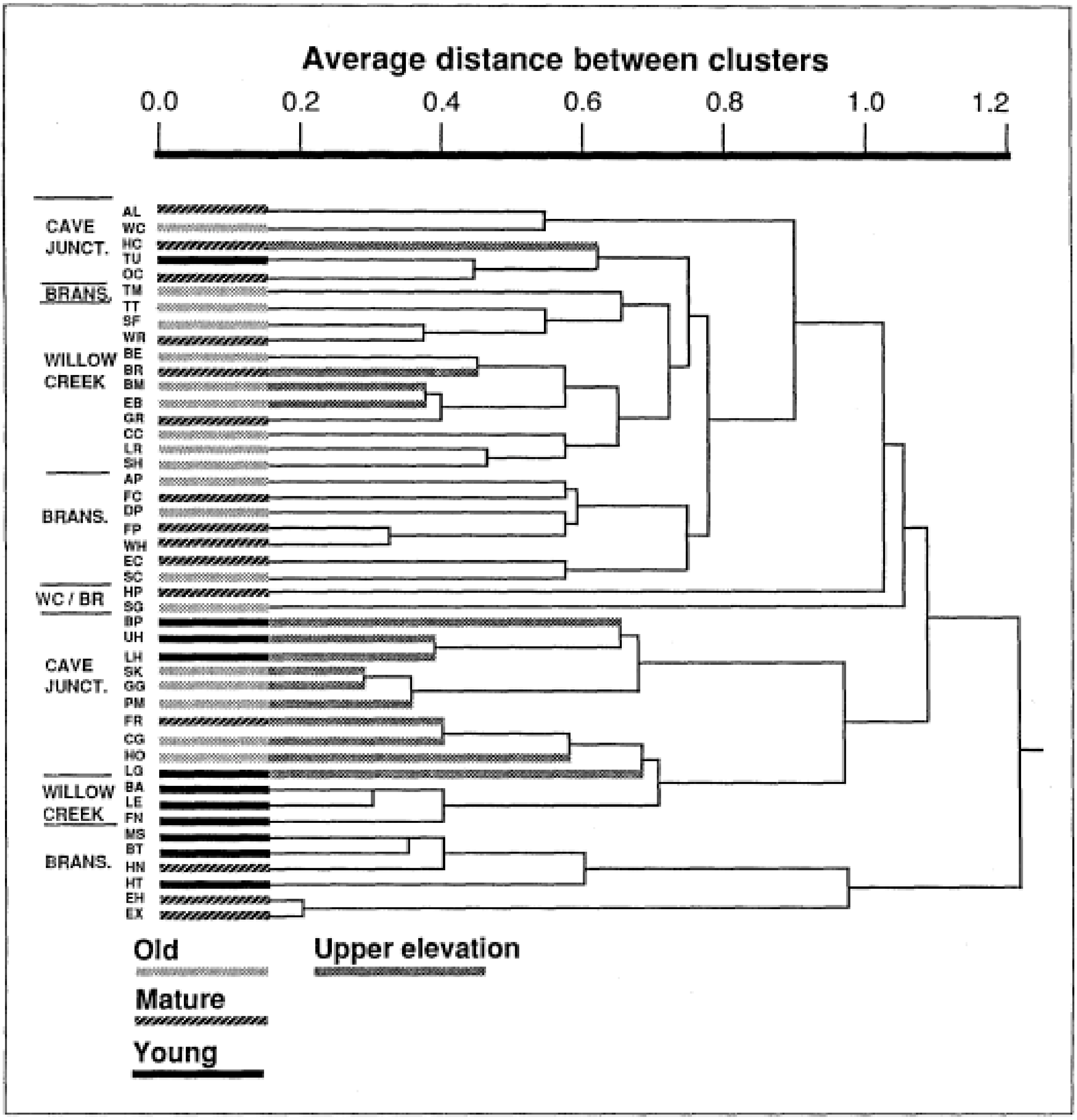

Figure 4-Cluster diagram of the 45 stands based on the abundance of the 21 most common bird species.

Table 5-Comparison of the correlation [a] between the abundance of small mammal captures and the age of the stand, amount of conifers, amount of hardwoods, and amount of hard and soft logs

Species	Age	Conifer	Hardwood	Hard log	Soft log
Snap traps					
Western red-backed vole	0.350*	0.302	–0.163	0.161	0.172
Deer mouse	.171	–.125	.114	.129	–.129
Pacific shrew	.236	.303	.333*	.242	.497*
Trowbridge's shrew	–.113	.010	–.222	.010	.466*
Piñon mouse	–.248	–.462*	.369*	–.048	–.026
Live traps					
Western red-backed vole	.600*	.204	–.181	.091	.045
Deer mouse	.223	–.123	.030	.053	–.254
Trowbridge's shrew	–.203	–.117	–.124	–.209	.370*
Piñon mouse	–.117	–.445*	.449*	.021	–.117
Chipmunks	.265	–.461*	.419*	.138	.046
Pitfall traps					
Western red-backed vole	.158	.266	–.231	–.151	.307
Deer mouse	–.045	.290	–.193	–.153	.212
Pacific shrew	.112	.281	–.134	.185	–.146
Trowbridge's shrew	.141	.355*	.498*	–.032	.303
Piñon mouse	–.142	–.083	–.210	–.130	.241

[a] Significant linear correlations ($P \leq 0.05$) are indicated with an asterisk.

red-backed vole, deer **mouse, pinon mouse,** Pacific shrew, Trowbridge's shrew, and the combined chipmunk species. In addition, two squirrels and the chipmunks were counted during the bird counts.

We captured most species of mammals in all three areas, and by all three techniques, with the exception of some of the rarer species (table 4). We have discussed at length, the strong differences among the different capture methods (Taylor and others 1988). Among the mammals, the western red-backed vole had significantly fewer captures in the more southerly Branscomb region than in the central and northern regions. We have reported (Taylor and others 1988) that the vole's abundance was significantly correlated with true firs found on 11 stands in the north and none in the south. The two mice species were significantly more abundant in the south than in the north. The shrews were equally common in all regions, and the sample sizes of other species, including the chipmunks, were perhaps too small to demonstrate the effect of region.

The western red-backed vole was the only captured species that had a significant positive association with the age of the forest stand ($P < 0.05$; table 5), which confirms previous studies (Raphael 1988, Raphael and Barrett 1984) in the Willow Creek area. Bird count data indicates that Douglas' squirrel was also positively associated with stand age, and this greater abundance in older stands was consistent among the regions (table 2). The abundance of the chipmunk species and gray squirrel were related to region. Chipmunks and Douglas' squirrel were more common at Cave Junction, and the gray squirrel was more common at Branscomb.

The pirlon mouse had the clearest association with hardwood density and clearly lacked association with stands that included conifers (table 5), judging from captures in both snap and live traps. The Pacific shrew was positively associated with hardwoods and soft logs, and Trowbridge's shrew was also positively associated with soft logs. The combined chipmunk species were positively associated with hardwoods, and negatively with conifers.

Discussion

Total species richness of birds in our stands is much higher than for stands discussed elsewhere in this volume that are located farther north in Oregon and Washington. We suspect this results from the much greater diversity of vegetation in our stands (Bingham and Sawyer, this volume) that resulted from a greater abundance of hardwood. Indeed, a few of our bird species showed a close association with hardwoods in general. A matter of concern is that present logging practices in our region are directed towards eliminating hardwoods as an important component of the commercial forests. As Raphael (1987) has shown, and our data reaffirm, the numbers of many species would probably be greatly reduced if this strategy was successful. Perhaps fortunately for the wildlife, silviculture is an imperfect art and many harvested conifer stands are regenerating into stands with a high per-

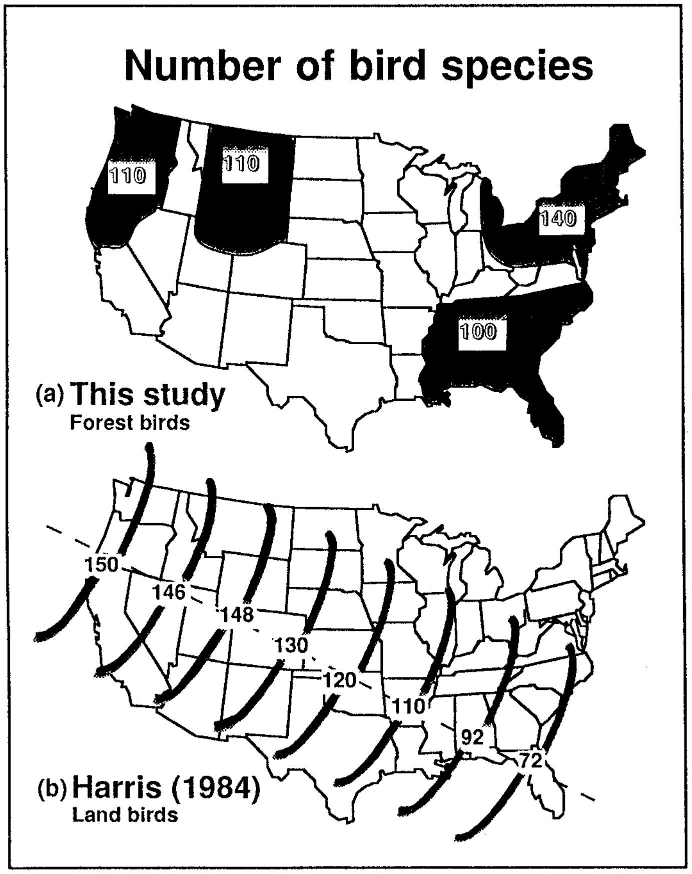

Figure 5-Number of breeding forest birds by geographic region, (a) taken from Blom (National Geographic Society [19871), and (b) Harris (1984).

centage of hardwoods. We are experiencing a permanent loss of mature hardwoods, however, which may profoundly affect some animal species.

Harris (1984) points out that Pacific Northwest forests were the richest in North America in terms of bird species, based on MacArthur and Wilson's data (1967) (reproduced in fig. 5b). MacArthur and Wilson, however, were discussing all breeding birds, not just forest birds. Our recalculation of the number of breeding forest birds (fig. 5a) showed that the northeastern United States is the richest area in the North America, with about 140 species, and the Rocky Mountain area and the Pacific Northwest are tied at about 110 species each.

Although the Pacific Northwest is not particularly rich in forest-bird species, it does have many species endemic to the area. A comparison (based on the range maps of the National Geographic Society 1987) of the endemic species largely confined to the four regions of figure 5a showed a striking contrast. The Rocky Mountain area has no species confined to that region's forests. The northeastern region of the United States has only the golden-winged warbler. Only the southeast and the northwest have a significant number of endemic forest birds. The southeast has six (red-cockaded woodpecker, ivory-billed woodpecker, brown-headed nuthatch, Swainson's warbler, Bachman's warbler, and Bachman's sparrow) and the northwest has seven (Vaux's swift, rufous hummingbird, white-headed woodpecker, red-breasted sapsucker, hermit warbler, and chestnut-backed chickadee). That most of the endemics in the southeast are now extinct, rare, or declining, may not be irrelevant because that region's old-growth forest was essentially eliminated during the last century.

Many species in our study showed affiliations with stand age. Three birds were significantly more abundant in old-growth forests than either the young or mature stands: the hairy woodpecker, western flycatcher, and brown creeper. Many other birds were more common in the mature and old-growth stands than in the young stands. For these species, older forests are probably a preferred, but perhaps not required, forest configuration. Age was a major factor only when the difference between the young forests on the one hand, and the combined mature and old-growth forests on the other is considered. Between the two older categories, the species composition was quite similar.

Raphael (1984, 1987) and Raphael and Barrett (1984) conducted a study of forest birds and mammals and their standage associations in one of our study regions near Willow Creek, California. Raphael (1984), compared stand age with the abundance data from a single year for birds in the Willow Creek area. He found 25 significant relations (see table 2). Of the 25 species, our data agreed for 8 species, but disagreed for 7 species. In these seven cases, Raphael (1984) found a negative relation with stand age, and we found a positive relation. We found no significant relation for the remaining 10 species. We are not certain of the reason for this disparity of results, although methods did vary because our study covered a wider geographical range over a period of 2 years, and Raphael's (1984) study used 136 study plots from a single year.

Of the mammals we studied, only the abundance of western red-backed voles and Douglas' squirrels were positively associated with the age of the forest stand. Raphael (1988) found both species associated with older stands. He found 10 mammals that were positively correlated with stand age. Voles had by far the strongest relation to stand age. Perhaps the techniques we used did not adequately sample the larger carnivores that he found associated with stand age.

The stands chosen to represent different age-classes occurred naturally in the Cave Junction and Branscomb regions;4hat is, the young stands originated from fire or other catastrophic events, rather than as the result of timber harvests, and often were heterogeneous, with some structural and floristic com ponents that resembled old-growth stands. Scattered old trees and abundant dead-and-down material were sometimes present in young stands. These characteristics, which are usually absent from young stands that originated from clearcut timber harvests, may be important factors that affect patterns of bird abundance. Results from even-aged stands regenerating from a clearcut may be very different. The cluster analysis did, however, group the bird community of the natural, young Branscomb stands with the young Willow Creek stands that resulted from timber harvesting.

Our study area was fire-prevalent, and for that reason, it may have been a poor area for examining species that become dependent on old-growth stands. The stands in this southern area of Douglas-fir are subject to drier conditions and more frequent fires than their counterparts to the north. Many species may have developed more flexibility in the southern portion of the range of their habitat type.

When a species is more common in older forests, we cannot make a statement about the species' reliance on older stands without information on the activities of that species in younger stands. The three bird species of significantly greater abundance in old-growth forests (the hairy woodpecker, western flycatcher, and brown creeper) are a case in point. Some evidence (van Home 1983) indicates that a species' density is not necessarily correlated with habitat suitability. Thus, although these three species do attain moderate numbers in young and mature forests, those stands may include habitat that is unsuitable for breeding.

By far the most common habitat association pattern we detected was a positive association with conifers. The next most common, perhaps the converse, was a lack of association with hardwoods. Only seven bird and no mammal species were positively correlated with hardwoods. The association with conifers, both direct and indirect, might not be surprising given the conifer dominance of these forests. As we have suggested above, however, greater abundance of hardwood could be a factor in the increased species richness of the southern Douglas-fir forests. Raphael (1987) also found some species strongly associated with tanoak, an important hardwood species. This association included six positively correlated ($P < 0.05$) species, some of which were in agreement with our data. Raphael found one, the olive-sided flycatcher, positively correlated with tanoak, but our data indicated a negative correlation with all hardwoods. He also found the western flycatcher and hermit warbler positively associated with hardwood, but we did not. Our results agreed with Raphael's for only three species: the hermit thrush, varied thrush (only in the winter), and warbling vireo. The differences quite likely result from our method of combining all hardwood species, and Raphael's concentration on tanoak. They may, however, be related to the much larger geographic region included in our study. The strong geographic influence on patterns of species abundance within our study area has important management implications. We found that species abundances often differed significantly between regions in their relation to age (the ageregion interaction shown in table 2); that is, in one region the relation might be positive, in another negative, and in the third, have no pattern. These differences are to be expected because at the periphery of its range or habitat, a species is most likely to be constrained to a narrower range of environmental conditions than at the center. Land managers might find that, to maintain a species in a given region, quite different strategies of land use from those used in other regions might well be necessary.

Because many species' abundances are related to stand age and composition, further alterations of the landscape will likely result in profound changes in the abundance patterns of many of the species in the study area. This, however, will probably not result in any extinctions in the foreseeable future. For the great majority of the species in this study, the pervasive influence of stand age and composition on population levels should warn us that close monitoring of some species may be necessary. At the very least, periodic sampling should be conducted to determine the population status of species in the area.

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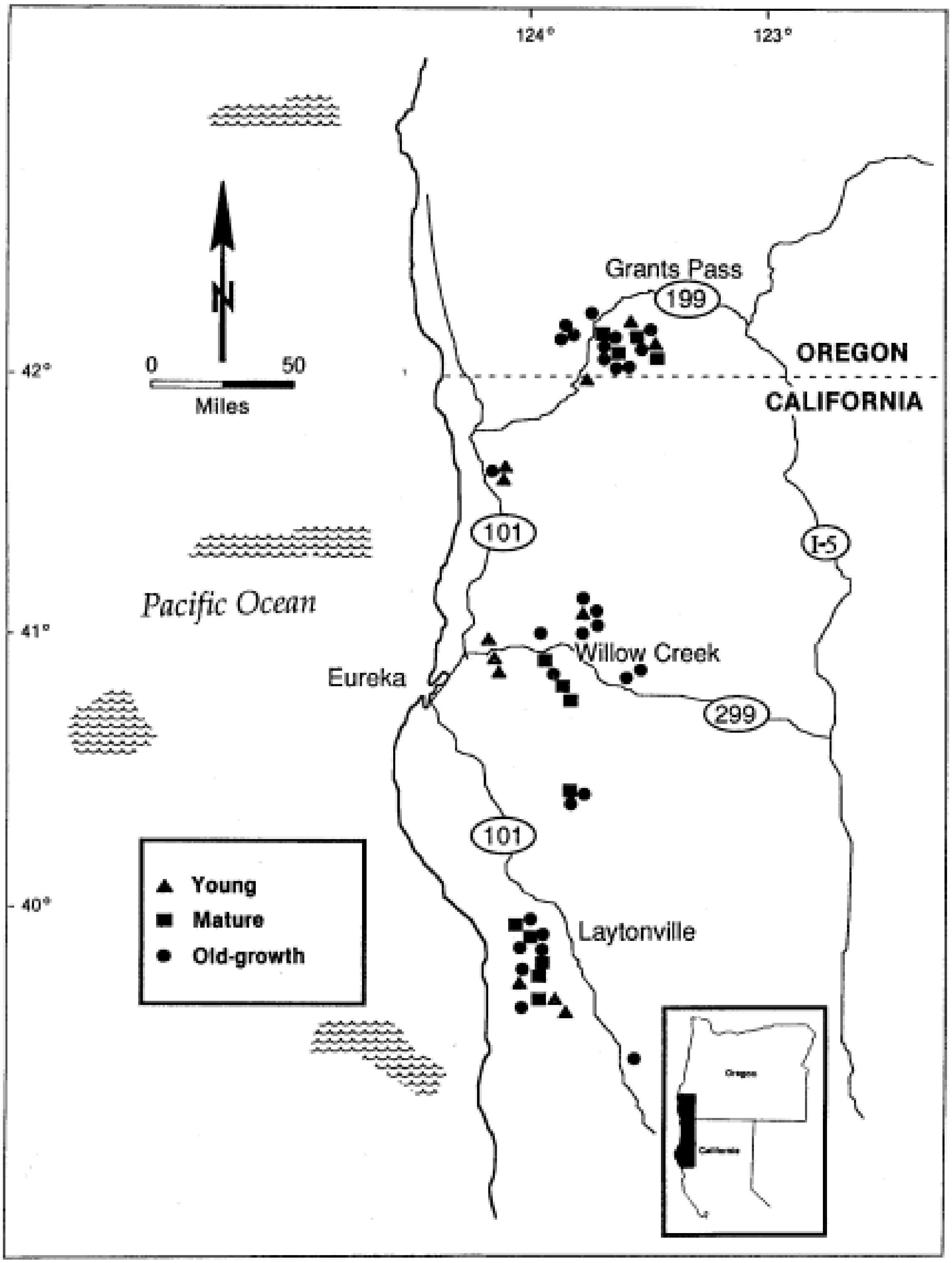

Location of study sites.