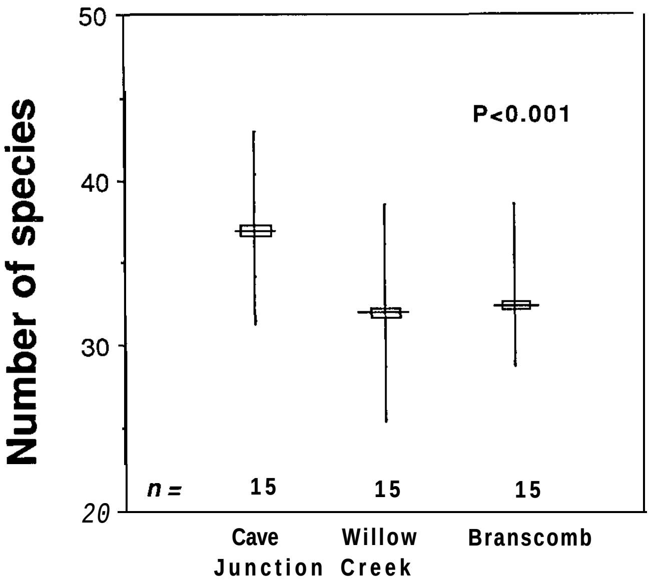

Figure 1—Comparison of the number of bird species by region. The means, standard errors, and ranges are shown for stands in each region. Sample size is shown below.

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.

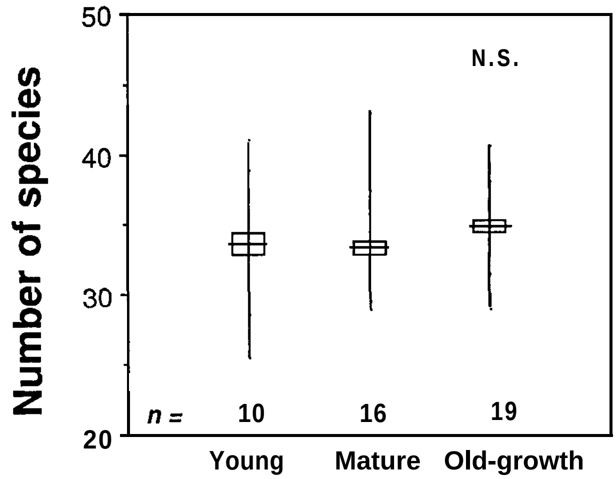

Figure 2—Comparison of the number of bird species by age-class. The means, standard errors, and ranges are shown for stands in each age-class. Sample size is shown below.

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 stands with more hardwoods (r = -0.53; P < 0.001).

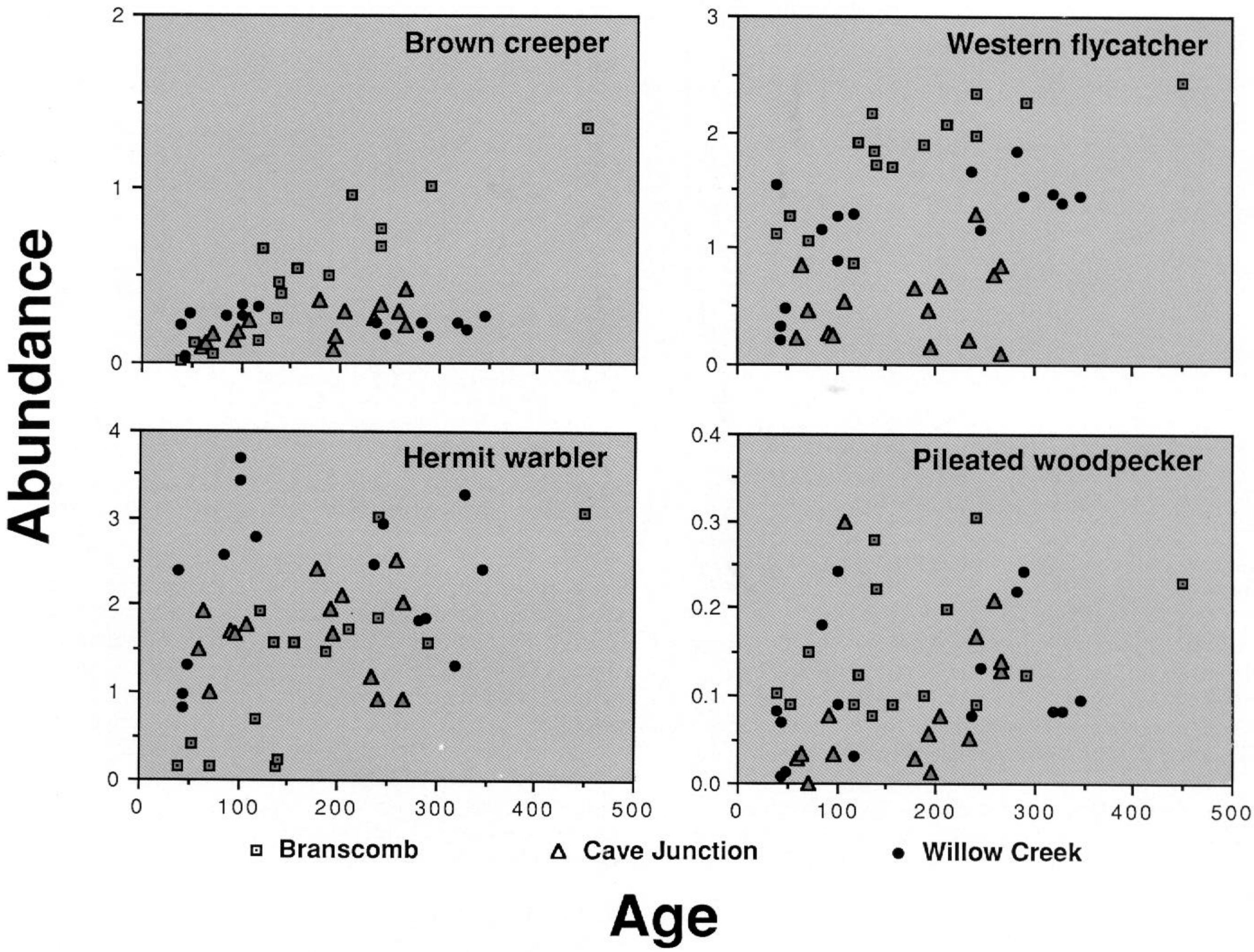

Figure 3—A comparison of the mean abundance of four bird species by stand and region with the square root of stand age as a continuous variable.

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 nuthatch, 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 associated 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

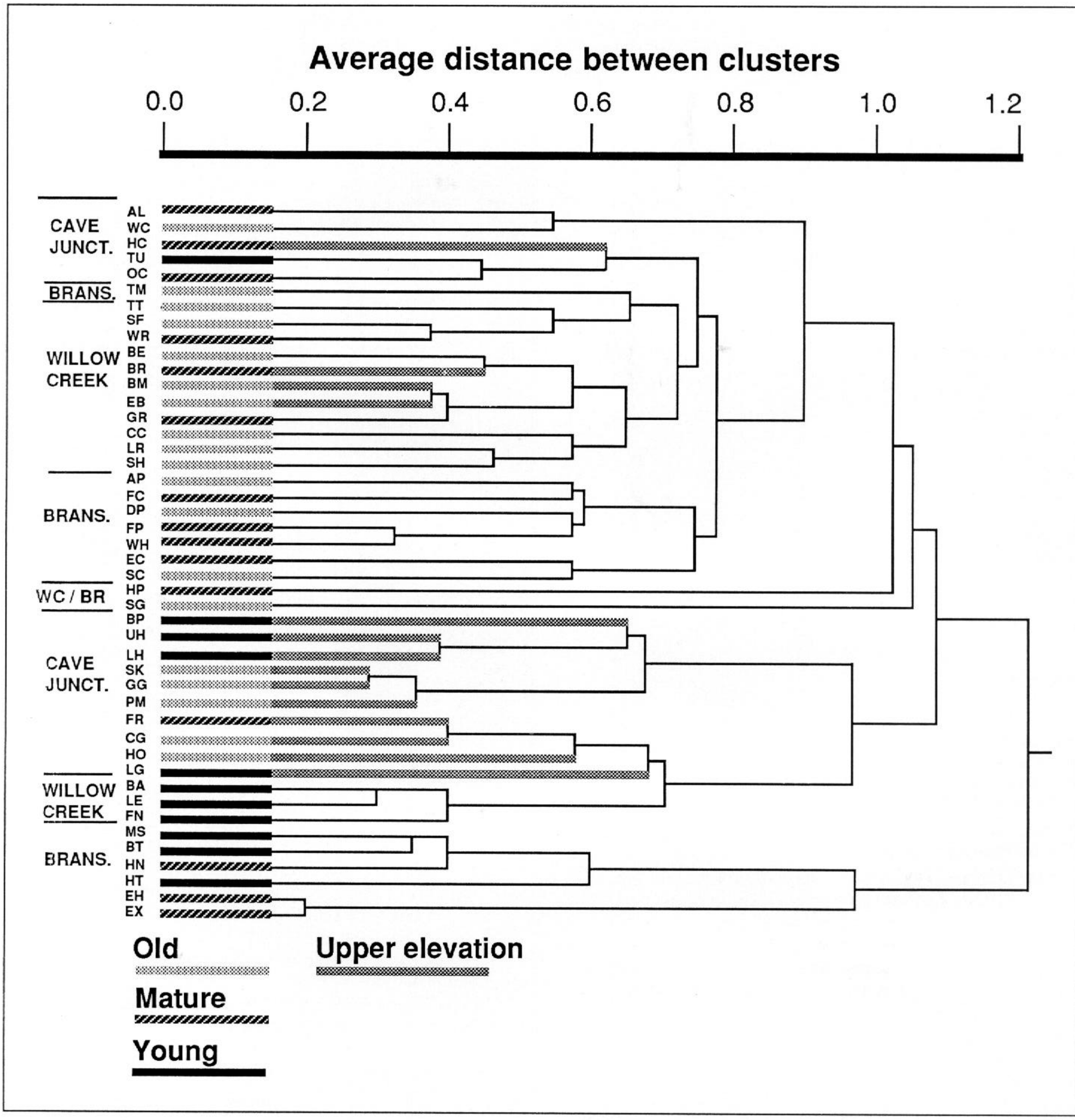

Figure 4—Cluster diagram of the 45 stands based on the abundance of the 21 most common bird species.

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, piñon 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 piñon 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-

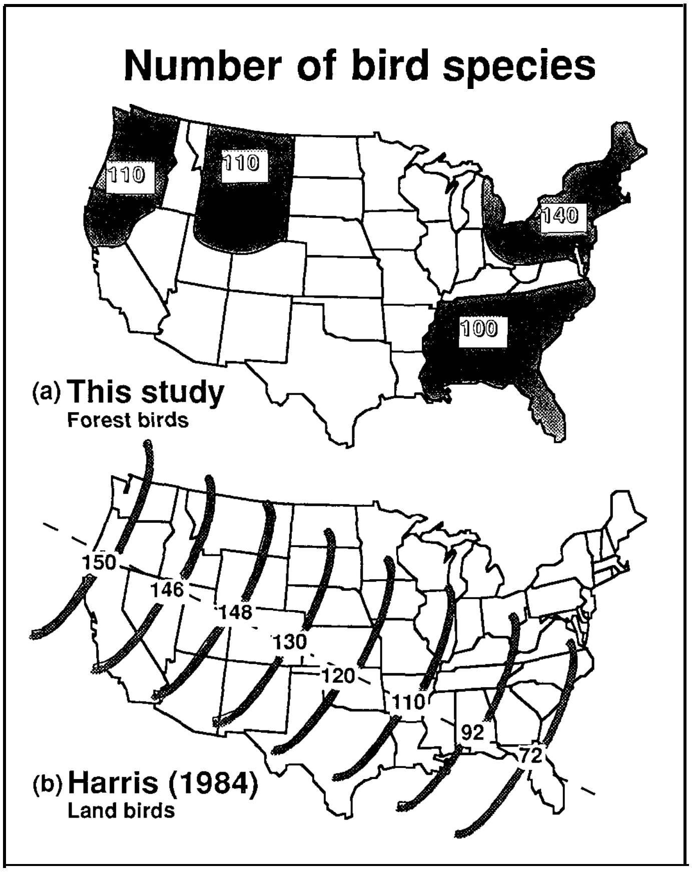

Figure 5—Number of breeding forest birds by geographic region, (a) taken from Blom (National Geographic Society [1987]), and (b) Harris (1984).

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 stand-age 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; that 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 comportents 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 age-region 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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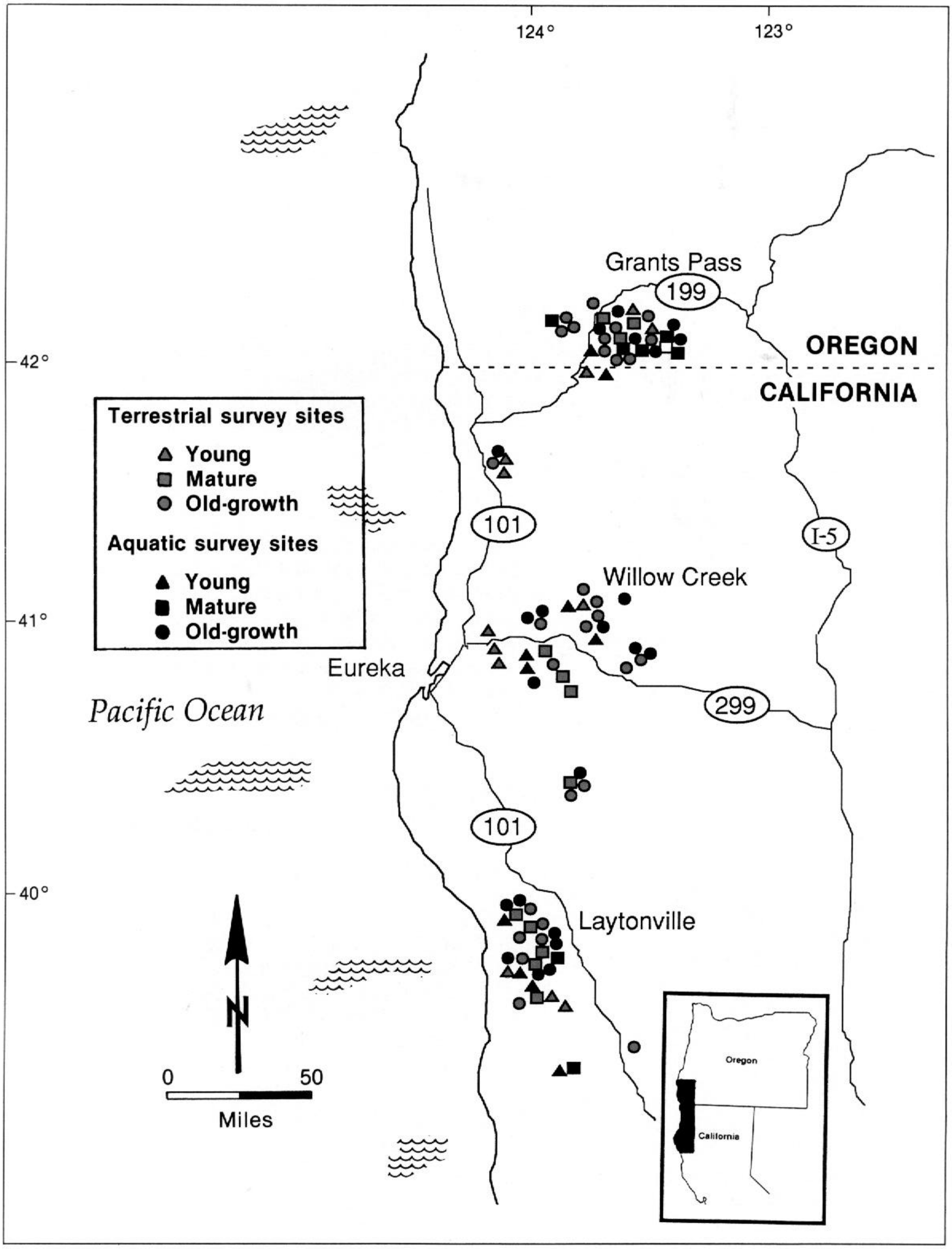

Location of terrestrial and aquatic study sites.

The Structure of the Herpetofaunal Assemblage in the Douglas-Fir/Hardwood Forests of Northwestern California and Southwestern Oregon

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Abstract

Terrestrial and aquatic herpetofauna were sampled by three methods, time-constrained searches, pitfall traps, and area-constrained searches from 1984 to 1986 in northwestern California and southwestern Oregon. The 54 terrestrial and 39 aquatic study sites were in Douglas-fir/hardwood forest stands that ranged in age from 30 to 560 years. Results of these surveys are presented in terms of species richness, equitability, relative abundance, relative biomass, and macrohabitat and microhabitat associations.

Although species richness did not differ among forest age-classes, the composition of the herpetofauna was notably different. Old and wet sites had proportionately more amphibian species, and young and dry sites had proportionately more reptile species. Terrestrial salamanders were more abundant on old-growth than on young sites. We also found that structural components associated with older forests were the best predictors of increased numbers of salamanders. Analyses of microhabitat associations indicated that large, well-decayed logs were the most heavily used woody debris, though use of particular size- and decay-classes varied among salamander species.

Harvesting forests without immediately affecting herpetofauna is probably not possible; however, strategies can be developed to minimize long-term adverse effects. We provide a summary of management recommendations designed to assure long-term viablity of herpetofauna in areas subject to logging.

Introduction

Old-growth forests are a unique and complex ecosystem where many life forms occur in numbers disproportionate to their occurrence in other parts of their range (Thomas and others 1988), but the nature of the ecological dependencies (Ruggiero and others 1988) between these species and the ancient forest ecosystem are only beginning to be understood. More knowledge about the spatial and temporal distributions of species in old-growth and in younger natural and managed forests, and an understanding of habitat requirements and ecological interdependencies are required to make sound decisions that assure healthy forests in the future.

We describe the species composition and relative abundance of members of the herpetofaunal assemblage in the southern portion of the Douglas-fir region, with a focus on how presence and abundance are related to forest age and structural aspects of the forest habitat.

Heatwole (1982), in a review of available literature on the structure of temperate and tropical herpetofaunal assemblages, noted how little is known about them and their relation to the larger community of organisms that constitute a complete ecosystem.

Pough (1980, 1983) outlined some of the unique adaptations of herpetofauna that illuminate their critical role in ecosystem dynamics and place them in a larger ecological context. Their small body size and elongate body form, energetically unfeasible for endotherms, permits them to use space and exploit food resources unavailable to other vertebrates. Their ectothermic nature facilitates a life of low energy demand. They are better suited than endotherms to periods of limited food, water, or oxygen. Endotherms are generally viewed in terms of the energy they consume, but reptiles and amphibians are more realistically considered in terms of the biomass they produce and make available to other trophic levels (Pough 1980: 104). These small vertebrates comprise an essential trophic level in the ecosystem, where invertebrate biomass is converted to vertebrate biomass far more efficiently than by endothcrms. Pough, comparing the efficiency of secondary production of endotherms and ectotherms, noted that the "...net long-term conversion efficiencies of amphibians and reptiles are many times greater than those of birds and mammals. The ecological significance of this efficient biomass production is enormous" (Pough 1980: 102).

Methods

Study Area

The study was conducted in Douglas-fir/hardwood forests of the Klamath Mountains and Coast Range of northwestern California and southwestern Oregon; the southern portion of the Oregonian Province (Udvardy 1975). Fifty-four terrestrial study sites, ranging in size from 21 to 150 ha, and 39 aquatic study sites (15-m lengths of second- or third-order streams) were sampled (see frontispiece and appendix table 9). For site selection procedures see Bingharn and Sawyer (this volume). Forests at the terrestrial sites ranged in age from 40 to 450 years; forests at the aquatic sites ranged in age from 30 to 560 years.

Herpetofauna Sampling

Four methods were used to sample the species composition, abundance, and biomass of the herpetofauna; time-constrained searches (timed searches), pitfall traps (pitfall), area-constrained searches (area searches), and opportunistic observations. These methods are described in more detail elsewhere (Bury and Raphael 1983, Corn and Bury 1990, Raphael and Rosenberg 1983, Welsh 1987). **Timed searches** recorded the search effort of two to three persons while they moved about the forest at random examining all microhabitats encountered, raking through litter, turning rocks and logs, tearing open decomposed logs, probing in vegetation, and so on. The clock was stopped when animals were encountered and while data were gathered. Our timed searches differed from those of Corn and Bury (1990) in that we searched seeps and springs in addition to rocks, logs, bark, and litter. **The pitfall** method consisted of trap grids with 36 traps spaced at 15-m intervals in a 6 x 6 arrangement. Traps were made of two, number 10 tins taped together and buried with the lip at the groundline and concealed by a cover of bark or cedar shake propped above the ground.

Terrestrial sites were sampled with timed searches, pitfalls, and opportunistic observations. We conducted four person-hour timed searches on each of 54 sites from April to June of 1984 and 1985, and on a subset of 30 sites from April to May of 1986. Our combined effort for timed searches totaled 552 person-hours. We ran 36-trap pitfall grids on 49 sites in October and November of 1984 for 50 nights and October of 1985, for 30 nights. The total pitfall effort equaled 141,120 trap-nights. Twenty-six amphibians and reptiles were recorded by opportunistic observation during sampling for other vertebrate groups or while vegetation data were collected.

Area searches were only done at aquatic sites. Our sampling of aquatic habitats consisted of area-constrained searches of 39 second- or third-order streams (Strahler 1952) on or near the terrestrial sites. We selected three 5-m reaches 1 to 3 m wide along each stream by walking 50 m upstream from the nearest trail or road access for the first reach, and 50 m from the top of the previous reach for subsequent reaches. Stream searches occurred during the summers of 1984 and 1985. The method consisted of mapping each reach to scale in order to plot captures, then methodically and sytematically searching all substrates, with catch nets placed downstream to capture dislodged animals.

Measurements of Forest Landscape, Structure, and Composition

Forest age- and moisture-classes-Sites were grouped into three forest age-classes: young, mature, and old-growth; and old-growth sites were classified into three moisture-classes: wet, mesic, and dry. Forest age was determined by tree

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