

Table 8—Results (*P*-values) of chi-square analyses comparing logs where salamanders were captured to the distributions of logs in different size- and decay-classes^a

Species	Size-class (conifers) ^b							Size-class (hardwoods)							Total
	1	2	3	4	5	6	7 ^c	1	2	3	4	5	6 ^c	7 ^c	
Clouded salamander	***	***	0.35	*	*	*	—	***	***	0.36	***	***	—	—	***
California slender salamander	***	***	***	*	***	***	—	***	0.09	.72	0.47	***	—	—	***
Ensatina	0.31	***	**	0.30	***	***	—	***	**	.22	***	***	—	—	***
Del Norte salamander	***	***	**	*	.36	.27	—	***	.41	.13	.27	.73	—	—	***
Total herpetofauna	*	***	***	.71	***	***	—	***	***	.85	***	***	—	—	***

Species	Decay-class (conifers)					Decay-class (hardwoods)					Total
	1	2	3	4	5	1	2	3	4	5	
Clouded salamander	*	**	***	.25	***	*	.07	**	*	.46	***
California slender salamander	**	***	***	***	.07	***	***	.66	***	.29	***
Ensatina	***	***	***	***	.37	***	***	***	***	***	***
Del Norte salamander	.12	***	.05	*	.13	.12	*	**	***	***	***
Total herpetofauna	***	***	***	***	*	***	***	***	***	***	***

^a Expected values were calculated from an independent data set of structural variables measured on the stands where herpetofaunal sampling occurred. Species captured in significantly greater (+) or smaller (-) numbers than expected for each class are indicated by *'s (* = 0.05 > *P* > 0.01; ** = 0.01 > *P* > 0.001; *** = *P* < 0.001).

^b Size-classes of downed woody debris are presented in square meters and defined as follows: 1, 0 - 0.5; 2, 0.5 - 1; 3, 1 - 2.5; 4, 2.5 - 5; 5, 5 - 10; 6, 10 - 25; and 7, 25 - 50.

^c Not tested; no expected values available.

Herrington (1988) reported the Del Norte salamander as essentially restricted to talus habitat. We concur that rocky habitats are important for this species (see macrohabitat section, above), but we believe some clarification is warranted. All of our captures for the Del Norte salamander occurred on sites with talus, rock outcrops, or rocky soils. Within these areas, however, we also found this species using downed woody debris for cover. Sixty-two percent of our captures were associated with such material (fig. 3), and 5 percent were within decayed logs.

We have almost no knowledge of the importance of below-surface habitat use for forest salamanders (N. Scott, pers. comm.); however, our data indicate that large numbers of salamanders use the subsurface, surface, and above-surface habitats provided by downed woody debris. Similar results from other studies in comparable habitats (Aubry and others 1988; Bury and Corn 1988a; Corn and Bury, this volume b) support the conclusion that these habitat features are probably essential for many species of forest salamanders.

Size of woody debris cover—The highest capture rates of all species combined were in the smallest and the next two larger size-classes of both conifer and hardwood logs (fig. 4). Captures were significantly lower than expected in several of the intermediate size-classes and did not vary from expected captures in others (table 8). The most abundant downed woody materials on our sites were pieces in the 0.5- to 1-m² size-class (fig. 4), but the frequency of captures of herpetofauna for this size-class was significantly less than expected (table 8). Although we captured salamanders in the largest size-classes of both conifers and hardwoods, the independent data set from which we derived our expected values lacked sufficient numbers of logs in these classes to allow for statistical tests (fig. 4, table 8).

The slender salamander and ensatina occurred in patterns similar to that described for the total herpetofauna (table 8). The clouded salamander, however, apparently chooses the larger classes (table 8), particularly of conifer logs (fig. 4), consistent with the findings of Corn and Bury (this volume b). The

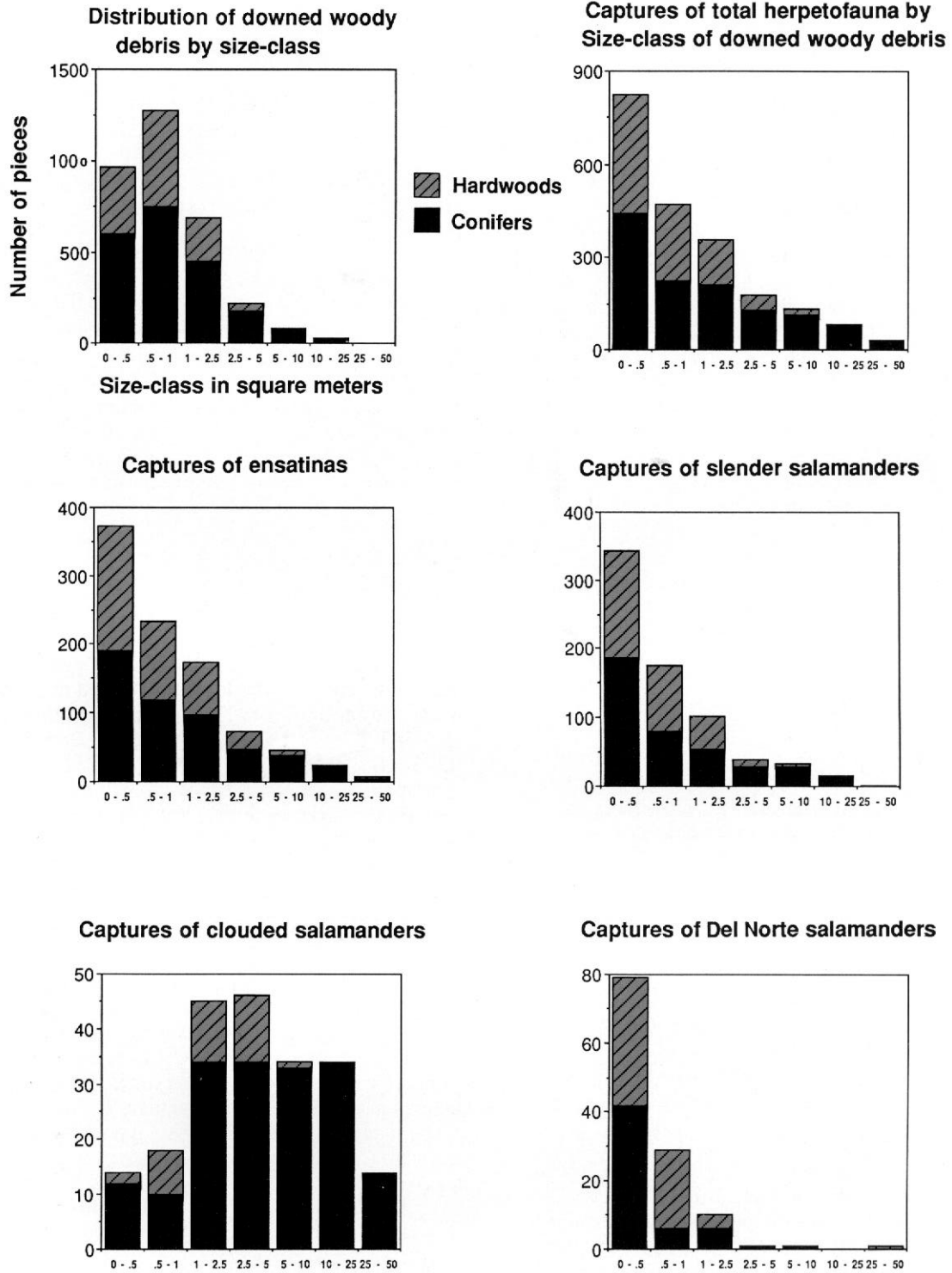


Figure 4—A comparison of the distribution of size-classes of hardwood and conifer downed woody debris (B. Bingham, pers. comm.), with the use of size-classes by the total herpetofauna (timed search) and the five most abundant salamander species.

Del Norte salamander occurred more often than expected under the smallest size-class of both hardwood and conifer debris, less than expected in intermediate conifer debris, and showed no deviation from expected in large conifer and all other hardwood classes (table 8).

Decay-class of woody debris-Our estimates for the amount of downed woody material (logs and branches-snags were not included) by decay-class indicated a nearly normal distribution from sound to rotten, with more conifer than hardwood pieces (fig. 5). Decay-class 3, characterized by logs with bark exfoliating and heartwood beginning to rot, contained the most pieces. In contrast, captures of the total herpetofauna by decay-class indicated significantly more captures than expected for class 4 conifer and class 4 and 5 hardwood logs, and fewer captures than expected in class 1, 2,3, and 5 conifer logs, and class 1,2, and 3 hardwood logs (table 8).

The slender salamander and ensatina occurred in patterns similar to those of the total herpetofauna with two differences. Both occurred as expected in class 5 conifer logs, and the slender salamander also occurred as expected in class 3 and 5 hardwood logs (table 8). The clouded salamander showed a strong preference for conifer logs (82 percent of all captures; fig. 5), and was captured more often than expected in decay class 3 (table 8). The Del Norte salamander was captured more often than expected under class 4 and 5 hardwood and class 4 conifer logs, and significantly less often in association with many of the sound-log classes (table 8).

Conclusions

Although we found 31 species of amphibians and reptiles over the course of this study, with 1 to 13 species per site, the herpetofauna of the region demonstrated low equitability, being dominated by a few species of salamanders. Species richness did not differ by forest age- or moisture-class, but species composition did. Several species of amphibian were rare or absent from young sites, while reptiles were relatively more abundant on these sites and on the old-growth dry sites.

We captured over 6400 individuals, of which 97.6 percent were amphibians, with salamanders comprising 88.1 percent. Terrestrial salamanders were more plentiful on old-growth sites, with four of eight species sampled at greater than incidental levels, significantly more abundant on these sites. Concurrently, we found greater relative biomass of amphibians on old-growth mesic sites and greater relative biomass of reptiles on young and dry sites.

We found that structural components (multiple regression analysis; macrohabitat variables) associated with older forests (Franklin and Spies, this volume) were the best predictors of increased numbers of salamanders.

Our analysis of microhabitat associations indicated that large, well-decayed logs, both hardwood and conifer, were the most heavily used downed woody debris. We found that the pattern of use of woody debris varied considerably, both in size- and decay-class, by species of salamander.

Nineteen of the 31 species we detected were captured at incidental levels (table 2). Some of these species may be considered secondary elements of the forest herpetofauna- for example, the sagebrush lizard that invades open areas subsequent to harvesting. Others, however, were captured rarely, either because they were uncommon or because we lacked adequate methods to sample them- for example, snakes. We know little about these species' life histories, their relation with the forest environment, what constitutes a viable population, or how these populations respond to the conversion of old-growth forests to young, managed stands.

Management Strategies To Maintain a Viable Herpetofauna

An increasing body of evidence from research in forested habitats indicates a change in herpetofaunal species composition, reduction of numbers of species, and reduced abundance within species after logging (Bennett and others 1980; Blymer and McGinnes 1977; Buhlmann and others 1988; Bury 1983; Bury and Corn 1988a, 1988b; Bury and Martin 1973; Corn and Bury 1989; Enge: and Marion 1986; Gordon and others 1962; Herrington and Larsen 1985; Pough and others 1987; Ramotnik and Scott 1988; Welsh and Lind 1988). Forests cannot be harvested without affecting the herpetofauna, but we believe that it is possible to reduce long-term adverse effects. Area-specific strategies can be developed that take into account the natural history of local species of reptiles and amphibians and the particular habitat requirements of these species. With this knowledge, the timing and potential effects of harvest activities can be modified to ensure minimal impact and thus maintain the long-term viability of the herpetofauna.

Based on data reported here and previously (Welsh and Lind 1988) for northwestern California and southwestern Oregon and summarizing ideas presented by other authors cited above, we propose a four-part strategy to ensure the long-term viability of all elements of the local herpetofauna in areas subjected to logging.

Avoid riparian zones-Riparian zones are often the most species-rich (for all wildlife, not just herpetofauna), and their protection with no-cut buffer zones could maintain source populations and corridors for gene flow that would promote rapid repopulation once regeneration has created suitable habitat in harvested upland areas (see Bury and Corn 1988b Bury and others, this volume b; Gilbert and Allwine, this volume c).

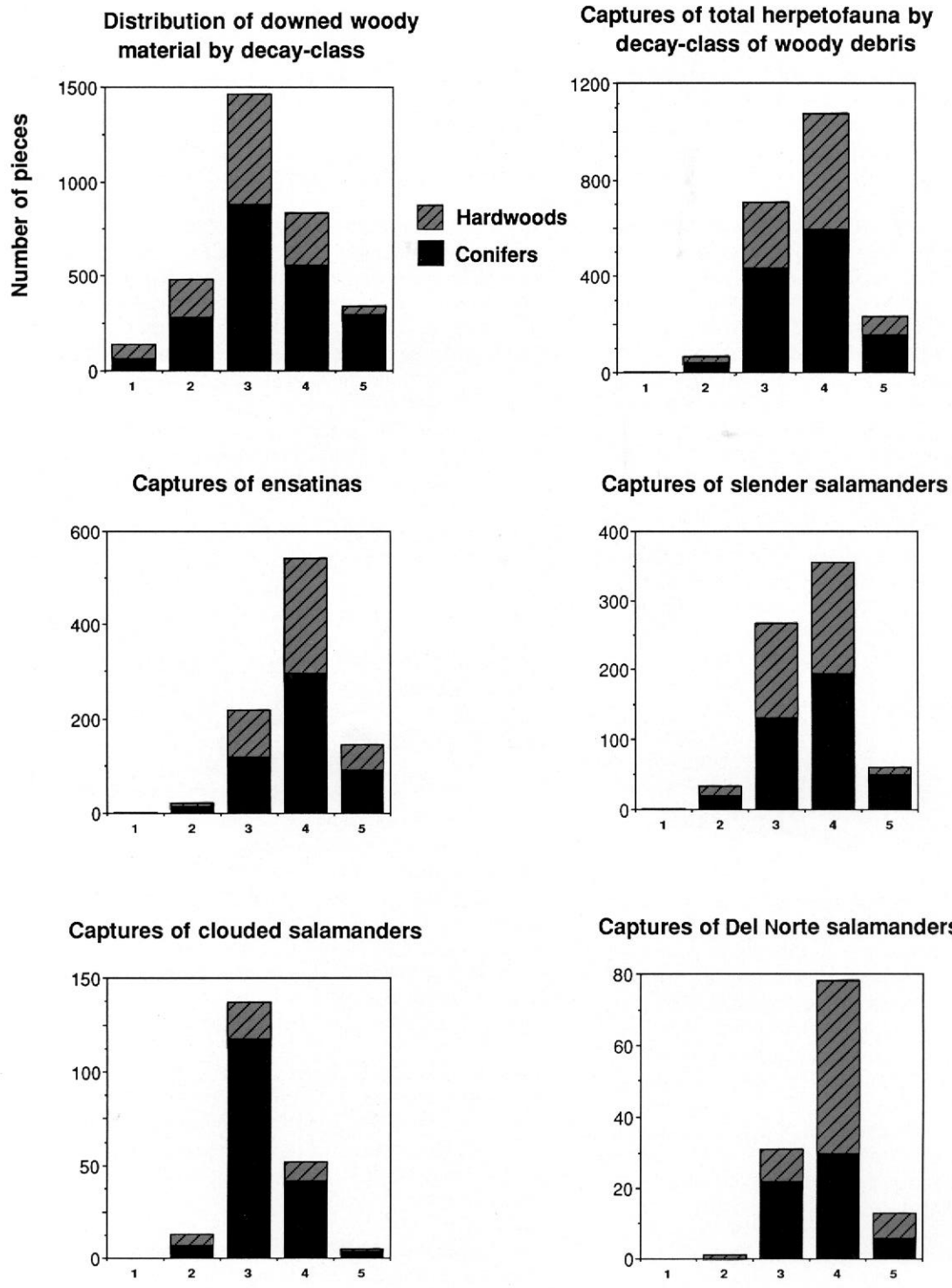


Figure 5—A comparison of the distribution of decay-classes of hardwood and conifer downed woody debris (B. Bingham, pers. comm.), with the use of decay-classes by the total herpetofauna (timed search) and the five most abundant salamander species.

Protect special habitats—Protecting special habitats includes springs, seeps, and other headwater habitats; large rock outcrops; talus slopes; ponds, and unique patches of habitat that are critical to certain highly sensitive species (for example, the red-legged frog, Olympic salamander, tailed frog, and Del Norte salamander) (see also Bury 1988; Bury and Corn 1988b; Bury and others, this volume a, b; Corn and Bury 1989; Gilbert and Allwine, this volume c; Herrington 1988).

Provide microhabitat—For forest herpetofauna, providing microhabitat means managing for downed woody debris. Almost all species of forest herpetofauna use woody debris at some stage, and many species use it throughout their existence, for cover, foraging, or nesting. After logging, an abundant amount of woody debris should be left, in all sizes and decay-classes, including both hardwoods and conifers when present, to facilitate the recovery of the terrestrial herpetofauna and other small vertebrates (see also Aubry and others 1988; Bury and others, this volume a; Corn and Bury, this volume b). The simplest approach is to leave all downed woody debris that was present before harvesting.

Minimize direct Logging effects—Restricting tractor logging would minimize compaction of the soil, and cable logging in winter would have far less effect on hibernating herpetofauna (Ramotnik and Scott 1988). As much canopy as possible should be left to prevent drying of the soil and alteration of understory vegetation.

Acknowledgments

We thank the members of the field crews of the Pacific Southwest Forest and Range Experiment Station's Timber/Wildlife Research Unit for their help in collecting data: C. Barrows, W. Block, L. Brennan, K. Calabrese, K. Clough, D. Carle, S. Edwards, S. Goldwasser, P. Hall, M. Hamady, L. LaClaire, D. Lausche, P. Manley, W. McCleod, K. Milne, C. Ogan, P. Paton, K. Purcell, T. Quinn, M. Rassmussen, R. Reynolds, H. Sakai, A. Schaffer, K. Schmidt, J. Sterling, C. Taylor, D. Taylor, and G. Therien. We also thank James A. Baldwin and Barry R. Noon for advising on statistical methods; Paul S. Corn, F. Harvey Pough, C. John Ralph, and R. Chad Roberts for their reviews of the manuscript (though all reviewer comments were not incorporated); and Dana L. Waters for his help with the figures. □

Appendix

Table 9—Study sites in mixed evergreen forests of northwestern California and southwestern Oregon (sites marked with an asterisk were included for total capture counts but omitted from further analyses—see text)

Sites	Age-class ^a	Moisture-class ^{b, c}	Location	County, State ^d	Elevation (m)
Terrestrial:					
Inland—					
Little Greyback	Y	M	T39S,R6W,S8	Jos,OR	1205
Tunnel	Y	M	T18N,R4E,S3&4	Del,CA	624
Waterman Ridge	Y	M	T7N,R5E,S15	Hum,CA	633
*Buck Peak	Y	M	T39S,R6W,S33	Jos,OR	1366
Althouse	M	M	T40S,R8W,S3	Jos,OR	427
Brush Mountain	M	M	T6N,R5E,S18	Hum,CA	1050
Gray	M	M	T5N,R6E,S4&5	Tri,CA	972
Hennessey Peak	M	M	T5N,R6E,S8&9	Tri,CA	949
Oregon Caves	M	M	T39S,R6W,S31	Jos,OR	872
Shelterwood	M	M	T1N,R4E,S34	Hum,CA	1022
*Left Hand	M	M	T40S,R6W,S23	Jos,OR	1362
*Upper Horse	M	M	T40S,R6W,S16	Jos,OR	1502
Beartooth Mountain	O	W	T6N,R7E,S34	Tri,CA	1144
Brannon East	0	W	T6N,R4E,S13&24	Hum,CA	750
Cedar Creek	0	W	T7N,R5E,S30	Hum,CA	665
*California Greyback	0	W	T19N,R6E,S32	Del,CA	1556
*Frog Pond	O	W	T41S,R7W,S14	Jos,OR	1539
*Holcomb Peak	O	W	T39S,R6W,S9	Jos,OR	1411
*Serpentine Wet	0	W	T41S,R9W,S4	Jos,OR	549
Big Creek-East	O	M	T6N,R7E,S36	Tri,CA	1134
Clouded	O	M	T1S,R4E,S2	Hum,CA	961
Ladder Rock	0	M	T8N,R6E,S32	Hum,CA	805
spotted Owl	0	M	T1S,R4E,S2&3	Hum,CA	981
Tish Tang	O	M	T8N,R5E,S35	Hum,CA	680
Sharber	O	M	T6N,R6E,S7	Tri,CA	747
* Galleghy Grove	O	M	T41S,R7W,S8,9,17,18	Jos,OR	1334
*Page Mountain	O	M	T41S,R7W,S8	Jos,OR	1519
*Serpentine Mesic	0	M	T38S,R9W,S25	Jos,OR	527
* Skag Hope	O	M	T41S,R7W,S7	Jos,OR	1305
Happy Camp	O	D	T40S,R7W,S29&30	Jos,OR	1053
South Fork	0	D	T6N,R6E,S31	Tri,CA	659
Waters Creek	0	D	T36S,R7W,S28,29,32,33	Jos,OR	614
*Serpentine Dry	0	D	T38S,R8W,S29	Jos,OR	544
Coastal—					
Bald Mountain	Y	M	T6N,R3E,S17&20	Hum,CA	846
Barnes Thirty	Y	M	T22N,R16W,S29&32	Men,CA	467
Fawn Prairie	Y	M	T7N,R2E,S25	Hum,CA	750
Homestead	Y	M	T21N,R16W,S13&24	Men,CA	726
Lord Ellis	Y	M	T6N,R3E,S8&17	Hum,CA	778
Mud Springs	Y	M	T21N,R15W,S13&24	Men,CA	689
Seed Tree	Y	M	T14N,R1E,S21&22	Del,CA	120
Shelterwood Leave	Y	M	T14N,R1E,S27	Del,CA	120
Elder Creek	M	M	T22N,R16W,S28	Men,CA	555
Elkhom Xeric	M	M	T22N,R16W,S17	Men,CA	518
Fanny's Place	M	M	T22N,R16W,S21	Men,CA	445
Harwood's 90	M	M	T21N,R15W,S23	Men,CA	695
White House	M	M	T22N,R16W,S21	Men,CA	427
Old Growth	O	W	T14N,R1E,S21&28	Del,CA	53
Skunk Creek	O	W	T22N,R16W,S29	Men,CA	529
Standley Grove	0	W	T21N,R16W,S26	Men,CA	481
Alpine	0	M	T22N,R16W,S20&21	Men,CA	444
Elkhom Hydric	0	M	T22N,R16W,S17	Men,CA	518
Fox Creek	0	M	T22N,R16W,S21&22	Men,CA	543
Ten Mile Creek	0	M	T22N,R16W,S15&16	Men,CA	445
Darby's Place	0	D	T18N,R13W,S1&2	Men,CA	587

Table 9—continued

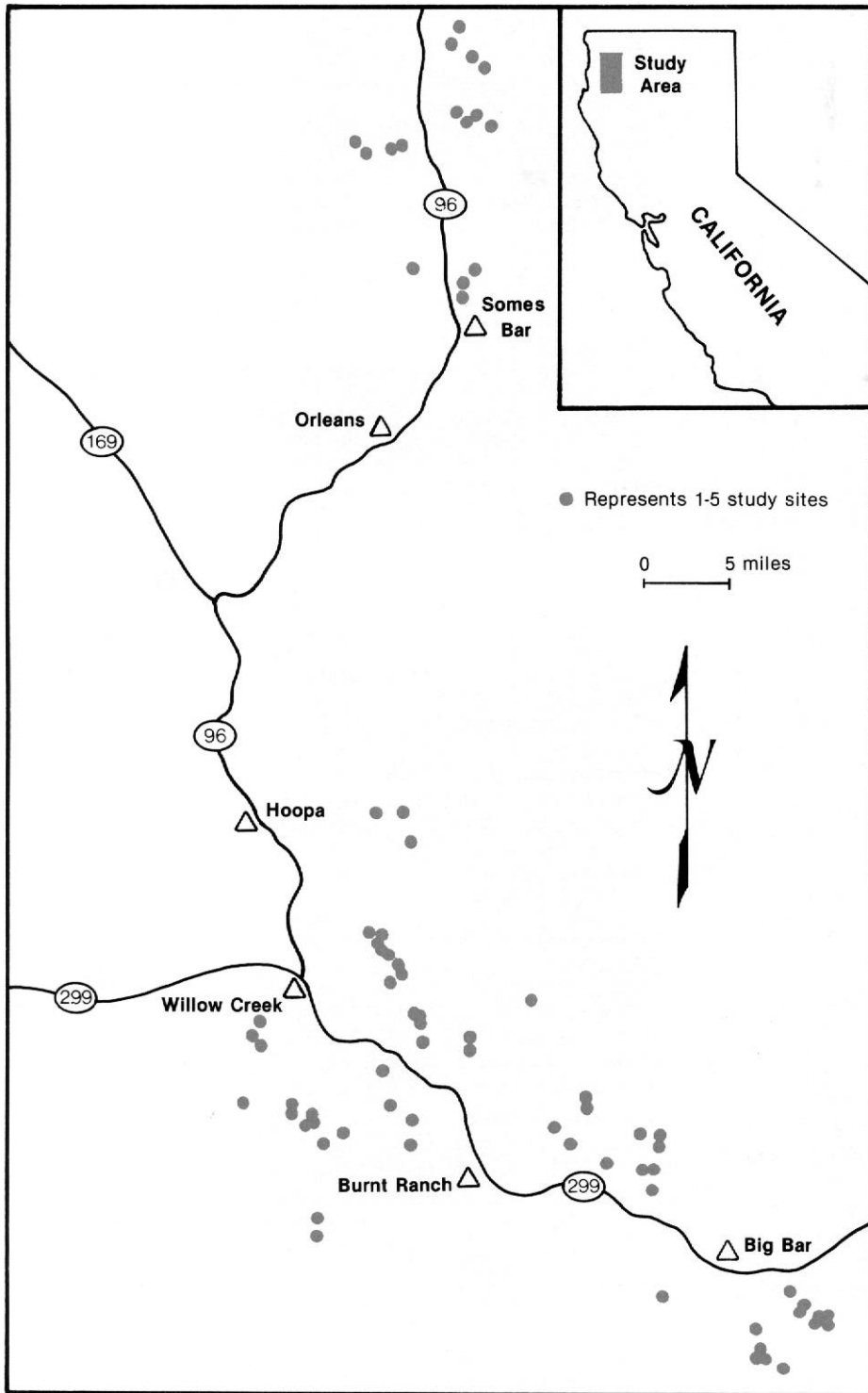
Sites	Age-class ^a	Moisture-class ^{b, c}	Location	County, State ^d	Elevation (m)
Aquatic:					
Ammon—North	Y		T5N,R5E,S11	Hum,CA	549
Barnwell Creek	Y		T22N,R16W,S21	Men,CA	427
Bybee Creek	Y		T19N,R5E,S33	Del,CA	671
Coon Creek	Y		T7N,R5E,S15&16	Hum,CA	213
Four Mile Creek	Y		T6N,R5E,S20	Hum,CA	671
Hawkins Tributary	Y		T6N,R6E,S15&16	Tri,CA	488
Kenny Creek	Y		T21N,R16W,S14&15	Men,CA	472
Sixteen Gulch	Y		T18N,R15W,S31	Men,CA	171
Sugar Creek	Y		T22N,R16W,S29&32	Men,CA	466
Althouse—Main	M		T41S,R7W,S11	Jos,OR	1341
Althouse—West	M		T41S,R7W,S16	Jos,OR	1158
Bolan Creek	M		T40S,R6W,S31	Jos,OR	975
Chamberlin Creek	M		T18N,R15W,S27&28	Men,CA	244
Days Gully	M		T38S,R9W,S25&36	Jos,OR	526
Lefthand Creek	M		T40S,R6W,S23	Jos,OR	1361
Limestone Creek	M		T40S,R6W,S21	Jos,OR	1067
McKinley Creek-Upper	M		T22N,R16W,S21	Men,CA	445
Page Creek	M		T41S,R8W,S2	Jos,OR	561
Barney Creek	O		T5N,R5E,S32	Hum,CA	823
Big Creek—East	O		T6N,R7E,S36	Tri,CA	1133
Big Creek—Main	O		T6N,R7E,S24	Tri,CA	1067
Brannon Creek	O		T6N,R4E,S13&24	Hum,CA	750
Butte Creek	O		T1S,R4E,S2&3	Hum,CA	980
Campbell Creek	O		T7N,R4E,S23	Hum,CA	884
Cedar Creek	O		T7N,R6E,S26	Hum,CA	1006
Elder Creek	O		T22N,R16W,S34	Men,CA	533
Elk Creek	O		T40S,R5W,S12	Jos,OR	1463
Elkhorn Creek—Upper	O		T22N,R16W,S17	Men,CA	518
Elkhorn Creek—Lower	O		T22N,R16W,S17	Men,CA	518
Fox Creek	O		T22N,R16W,S21&22	Men,CA	543
Frog Pond Creek	O		T41S,R7W,S14	Jos,OR	1539
Happy Camp Creek	O		T40S,R7W,S29&30	Jos,OR	1053
High Prairie	O		T14N,R1E,S21&28	Del,CA	53
Horse Linto—East	O		T7N,R7E,S7	Hum,CA	1280
Little Creek	O		T40S,R5W,S6	Jos,OR	1402
Little Greyback Crk.	O		T39S,R6W,S8	Jos,OR	1205
McKinley Creek—Lower	O		T22N,R16W,S21	Men,CA	445
Paralyze Canyon	O		T22N,R16W,S34	Men,CA	533
Skunk Creek	O		T22N,R16W,S29	Men,CA	529

^a Age-class: Y - young, M - mature, O - old.

^b Moisture-class: W - wet, M - mesic, D - dry.

^c Aquatic sites were not assigned a moisture-class.

^d County, State: Del - Del Norte, CA; Hum - Humboldt, CA; Jos - Josephine, OR; Men - Mendocino, CA; Tri - Trinity, CA.



Location of study sites.

Vertebrate Species Richness Within and Among Seral Stages of Douglas-Fir/Hardwood Forest in Northwestern California

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Abstract

One objective of wildlife management programs in National Forests is maintaining diversity, often thought of as the number of species or "species richness." Regional (multistand or landscape) species diversity varies in relation to species richness within stands and by similarity of species composition among stands. To evaluate numbers of species of terrestrial vertebrates in Douglas-fir forests of various ages in northwestern California, I systematically sampled at 166 sites representing clearcut (<20 years old) through old-growth (>250 years) forest. Mean numbers of mammalian species differed among seral stages and was lowest in mid-aged stands. Reptilian species richness declined with stand age. Amphibian and avian species richness did not differ among stages. Mean similarity values of all taxa did not differ significantly when sites within stages or sites among stages

were compared. Thus, landscape-wide species richness was independent of the arrangement of seral stages. These results suggest that maximizing population sizes of selected species is a more useful management objective than maximizing species diversity.

Introduction

The National Forest Management Act of 1976 made maintaining biological diversity a prime consideration in multiple-use management of National Forests. Thus, what has been termed "biodiversity" is now a major national issue, as evidenced by the National Biological Diversity Conservation and Environmental Research Act (H.R. 4335) brought before the 100th Congress in 1988. An important, but by no means the only component of biological diversity is species richness, the total number of species in a given system. Conservation strategies for maintaining biodiversity have ranged between two extremes: managing only for threatened or endangered species and managing whole ecosystems or communities (Scott and others 1987, 1988). Managing to maintain species richness falls under the latter strategy; it is now one of the major goals of USDA Forest Service wildlife management programs (Salwasser and Tappeiner 1981, Siderits and Radke 1977, Thomas 1982).

Managing Douglas-fir forests of the Pacific Northwest is under intense scrutiny because of conflicts between logging and preservation of remaining old-growth stands (The Wilderness Society 1988, Thomas and others 1988). Part of this concern centers on the importance of old-growth forest to biological diversity (Harris 1984, Norse and others 1986). This paper reports the results of a study designed, in part, to investigate the contribution of old-growth forest to local and regional species diversity in northwestern California.

Methods

Study Area

Sites were within a 3900-km² area encompassing parts of the Klamath, Six-Rivers, and Shasta-Trinity National Forests in northwestern California. Forest cover-classified as Douglas-fir (Mayer and Laudenslayer 1988)-is described elsewhere (Raphael 1988a). Criteria for site selection included elevation from 400 to 1300 m, road access, freedom from scheduled timber harvest over the 3 years of sampling, location on National Forest land, relatively homogeneous forest cover, and absence of major confounding features such as streams, meadows >1 ha, and rock outcrops. In addition, sites were selected to fill an array of stand sizes and age-classes (Raphael 1984).

Stand Classification

Sites were classified into four seral stages based on years since cutting or an index of stand age. Clearcut sites (n = 20) were <20 years old, young sites (n = 37) were 50 to 150 years old, mature sites (n = 56) were 150 to 250 years old, and old-growth sites (n = 53) were >250 years old. The age index was calculated with a weighted average of estimated ages of all softwood trees <90 cm in diameter at breast height (d.b.h.) counted on four 0.04-ha circular plots and softwoods ≥ 90 cm counted on one 0.50-ha plot on each site. The average was weighted by multiplying the estimated age of each tree by its basal area, summing the products over all trees, and dividing the sum by total basal area. In this way, the numerous small trees had less influence on stand age than if each tree was counted regardless of diameter. Tree age was estimated from diameter at breast height, based on extensive tree-ring counts on file in District offices. Details of vegetation sampling methods and vegetation characteristics of each stage are reported elsewhere (Raphael 1988c).

Vertebrate Sampling

Vertebrate sampling methods are described elsewhere (Raphael 1984, 1988c; Raphael and Barrett 1984; Raphael and Mamot 1986; Raphael and Rosenberg 1983; Raphael and others 1986; Rosenberg and Raphael 1986; Taylor and Raphael 1988). Field sampling took place from September 1981 through September 1983. A standardized series of

techniques was used on each site. Sampling stations were located at or around the center of a site and were separated from adjacent sites by at least 360 m. Birds were counted at each site (only in the three oldest seral stages) in variable-radius circular plots (12 10-minute counts in each site, season, and year), insectivores and other small mammals were trapped at each site in pitfalls (10 2-gallon buckets per site, 2 x 5 grid, 20-m spacing, run continuously), and larger mammals were detected at each site by using a single smoked-aluminum station deployed in August and September 1981-83. In addition, subsets of sites in each seral stage were more intensively sampled by area- and time-constrained searches for reptiles and amphibians (0.12 ha per site in 1981, 4 person-hours per site in 1982, 1983), livetraps for small mammals (usually 100 25-cm Sherman traps per site, 10 x 10 grid, 20-m spacing, operated 5 nights in July 1981-83), and drift fence arrays for snakes (two 5-gallon buckets, connected by a 7.6-m x 50-cm fence with two 20- x 76-cm cylindrical funnel traps on each side of the fence center).

Data Analysis

Species richness-All observations were reduced to the presence or absence of each vertebrate species at each site, pooled over all years of study (1981-83). A matrix of 166 rows (= sites) and 218 columns (= species, including separate entries for birds in spring and winter) was constructed so that each cell (combination of site and species) contained a 1 if the species had been detected at that site or a 0 if it had not. Based on stand age, each site was also classified into one of four seral stages for calculating species richness in each seral stage. Total species richness in a stage was calculated by summing numbers of species detected at any site within each stage. Mean species richness by stage was calculated by counting all species occurrences for each site, then calculating mean counts per site within each stage.

Species accumulation curves were computed to evaluate the effects of sample size (numbers of sites) on species richness. A bootstrap procedure (Efron 1982) was used to generate pseudosamples of increasing numbers of sites from 1 to 50. At any particular sample size y, a site (row) was randomly drawn from the site-by-species matrix. Data were stored, then replaced, and a new row was randomly drawn and data were accumulated. This process was repeated y times, accumulated cell values > 1 were recoded to 1, and cells were summed across all species to calculate species richness. The entire cycle was repeated for a desired number of pseudoreplications, usually 500. The mean and standard deviation were calculated over all pseudoreplicates and a standard error of the mean was calculated (which equals standard deviation under bootstrap theory).

Mean species richness was plotted against number of sites for various combinations of taxa and seral stages. Nonlinear regression (SPSS/PC+, Version 3.0, Norusis 1988) was used to estimate parameters of the species-area curve $S = CA^z$, where S was species richness, A was the number of sites sampled, and C and z were regression parameters (Connor and McCoy 1979, Higgs and Usher 1980, Usher 1985). Equality of regression parameters was tested among curves for each age-class using Extra Sum of Squares (Draper and Smith 1966: 67).

Species similarity—To compare occurrences of species between sites or groups of sites, I computed Jaccard's index of similarity,

$$RI = 100 \frac{a}{a + b + c},$$

where a was the number of species present at both i and j , b was the number present at site i only, and c was the number at site j only (Pielou 1984: 57). This index has many desirable properties (see Bloom 1981, Huhta 1979, Wolda 1981): it is easy to interpret (the index value is the percentage of species common to both sites), it takes no account of species absent from both sites (presence data are unambiguous, whereas absence could mean the species could not survive at the site or it was absent merely by chance), and it is metric (similarity values behave like distances in Euclidian space).

Similarities were computed between all possible pairs of plots and then sorted into site-by-site comparisons within each age-class and comparisons across age-classes. Means and standard errors were calculated for each grouping. I also computed similarities for each within and between age-class comparison using a bootstrap procedure in which a site was randomly drawn, replaced, and compared with another randomly drawn site. Similarity was computed, and a mean and standard error were computed over the total number of pseudoreplications used in an analysis (usually 200). To evaluate the effects of sample size (number of sites) or similarity, I used bootstrap procedures based on increasing numbers of subsets of sites from two to the maximum number of sites in an age-class.

All bootstrap analyses were conducted with a PC-based FORTRAN program, available on request (Raphael and Brink, documentation on file).

Table 1—Total numbers of species detected in 4 age-classes of Douglas-fir forest, northwestern California, 1981-83

Group	Age-class ^a				Total
	Clearcut	Young	Mature	Old-growth	
Amphibians	9	12	11	10	12
Reptiles	12	13	13	11	16
	NA				97
Wintering-birds	NA	44	45	47	55
Mammals	26	28	33	29	38

NA = not available (see Marcot 1984).

^a Age-classes and number of sites sampled were clearcut stands (<20 years, $n = 20$); young stands (<150 years, $n = 37$ for amphibians, reptiles, and mammals; $n = 27$ for birds); mature stands (<250 years, $n = 56$); and old-growth stands (>250, $n = 53$).

Results

Species Richness

Observers detected 167 vertebrate species over all sites and years. Recorded numbers of species varied within species groups among age-classes (table 1), but these values are difficult to interpret because of differences in sampling effort (number of sites) among age-classes. A more meaningful measure is mean species richness (fig. 1), the average number of species detected per site in each age-class.

Number of amphibian species averaged 2.7 species per site; means did not differ among age-classes (Welch's $F = 0.22$, $P = 0.89$, fig. 1). Numbers of reptilian species averaged 2.6 species per site and varied among age-classes (Welch's $F = 25.6$, $P < 0.01$, fig. 1), declining from youngest to oldest sites. Multiple comparisons of means (Dunnett's (1980) T^3 , $P < 0.05$) showed significantly more species in clearcut, fewer in old growth, and no difference between young and mature sites. An average of 10.8 mammalian species were detected at each site, and mean numbers of species varied among age-classes (Welch's $F = 9.1$, $P < 0.01$). Lowest mean numbers were detected in clearcuts and young stands; means were significantly greater in mature and old-growth stands (Dunnett's T^3 , $P = 0.05$). Numbers of breeding avian species averaged 32.3 species per site; means did not differ among age-classes ($F = 0.13$, $P = 0.88$). Avian species richness averaged 15.0 species per site in winter, and means also did not differ among age-classes ($F = 0.96$, $P = 0.39$).

In comparing differences between age-classes, I found large numbers of species that were infrequently detected. Of 218 vertebrates (including birds in two seasons), 88 (40 percent) were observed on 5 percent or fewer sites (fig. 2). Thus, estimated species richness at any particular site was influenced by chance occurrence of rare species. To alleviate this problem, I calculated species accumulation curves across successively larger sets of sites within each age-class (fig. 3).

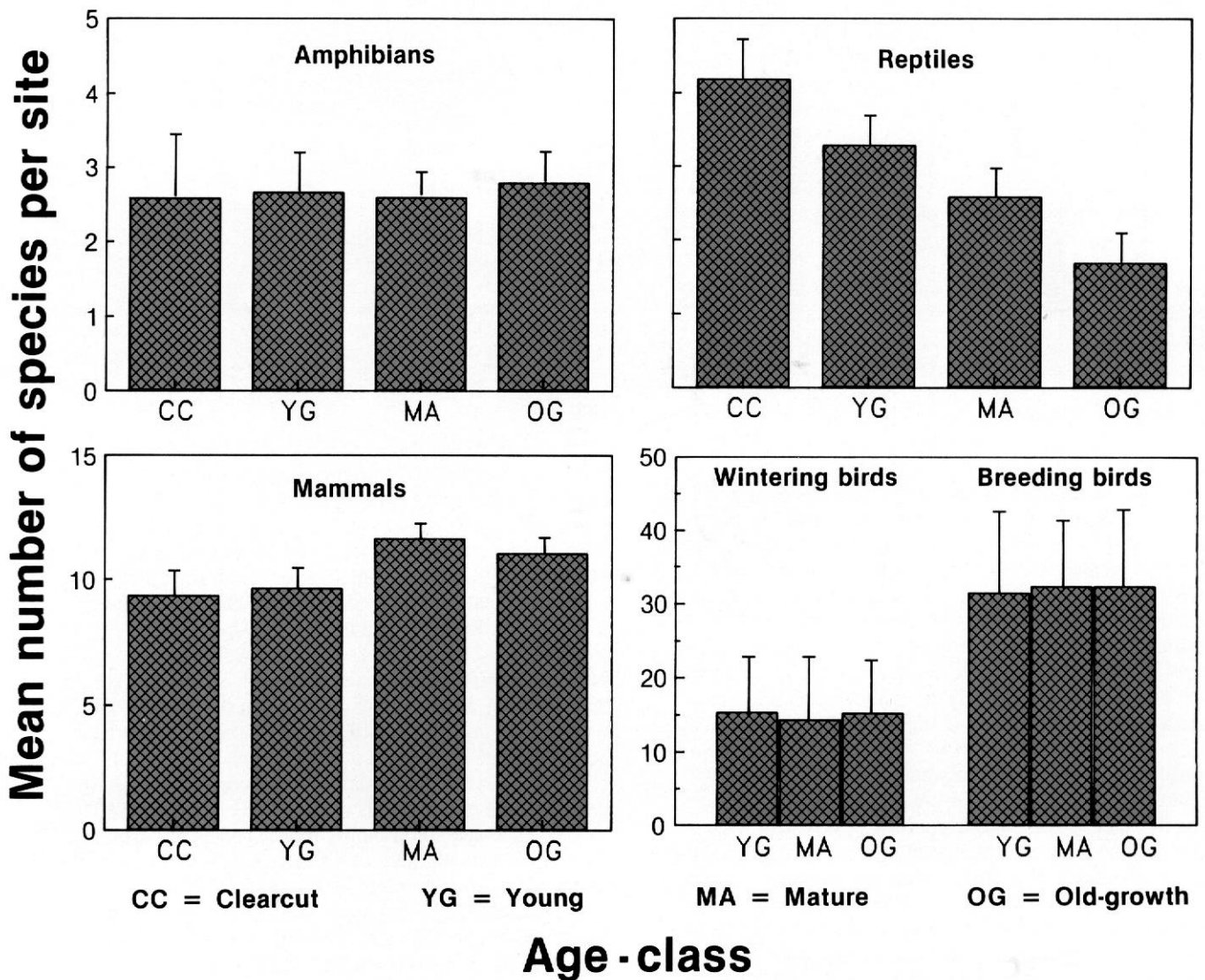


Figure 1—Mean numbers of vertebrate species detected in four age-classes of Douglas-fir forest, northwestern California, 1981-83. Age-classes are CC (clearcut stands, <20 years), YG (young stands 20 < x ≤150 years), MA (mature stands 150 < x ≤250 years), and OG (old-growth stands, >250 years); sample sizes are given in table 1.

For each species group, curves differed among age-classes (table 2). Extra sums-of-squares analyses for each species group rejected hypotheses of similar regression curves among age-classes (table 3). These analyses showed that, for each species group, C , z , or both differed significantly among two or more age-classes. Thus, rates that species accumulated as numbers of sites increased differed among at least two age-classes.

A more direct comparison, however, was to test differences in mean species richness at larger numbers of sites, illustrated for $n = 10$ sites (fig. 4). Means and standard errors were derived from a sample of 500 pseudoreplications of sites representing each age-class. For each species group, 95-percent confidence intervals around the mean for any age-class overlapped the means of each other age-class. This pattern held for each sample size tested up to the maximum number of sites.

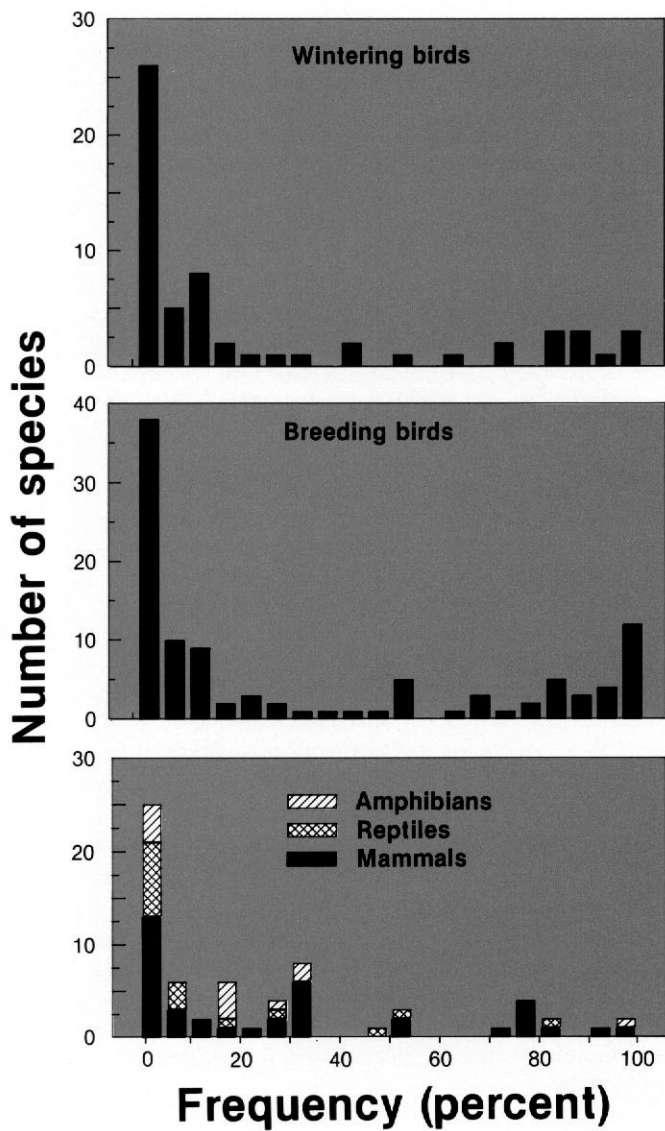


Figure 2—Frequency (percentage of sites on which a species was detected) of avian, amphibian, reptilian, and mammalian species on study sites ($n = 136$ for birds, $n = 166$ for all other groups) in Douglas-fir forests of northwestern California, 1981-83.

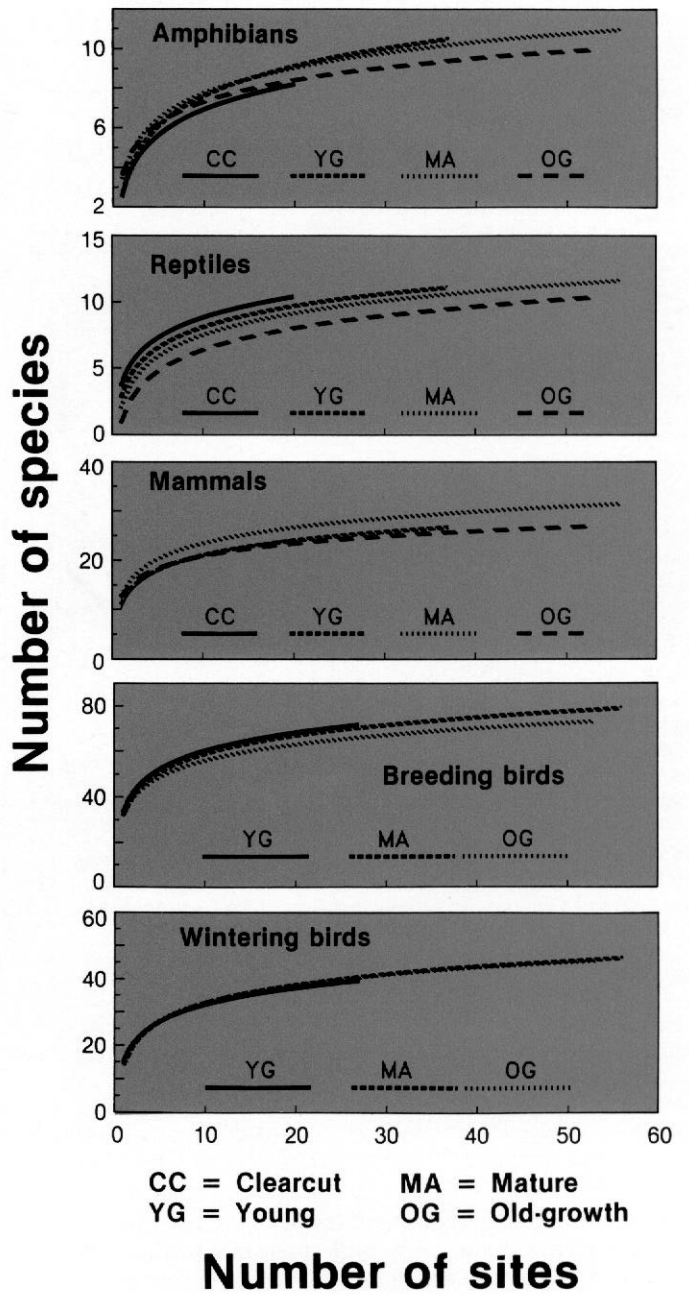


Figure 3—Species accumulation curves derived from bootstrapped samples of successively larger numbers of sites grouped into four age-classes of Douglas-fir forest, northwestern California.

Table 2-Regression parameters from nonlinear model relating species richness^a to numbers of sites among age-classes of Douglas-fir forest, northwestern California

Group	Age-class ^b	Parameter (SE) ^a		
		C	Z	r ²
Amphibians	Clearcut	3.31 (0.15)	0.31 (0.02)	0.96
	Young	3.76 (0.12)	0.29 (0.01)	0.97
	Mature	4.70 (0.19)	0.21 (0.01)	0.90
	Old growth	4.79 (0.20)	0.20 (0.01)	0.91
Reptiles	Clearcut	4.32 (0.05)	0.30 (0.00)	1.00
	Young	3.97 (0.07)	0.29 (0.01)	0.99
	Mature	3.69 (0.08)	0.29 (0.01)	0.98
	Old growth	2.80 (0.10)	0.34 (0.01)	0.97
Breeding birds ^c	Young	34.69 (1.20)	0.22 (0.01)	0.98
	Mature	35.33 (0.81)	0.20 (0.01)	0.99
	Old growth	34.01 (0.53)	0.19 (0.01)	0.99
Wintering birds ^c	Young	17.70 (0.55)	0.25 (0.01)	0.99
	Mature	18.72 (0.81)	0.23 (0.01)	0.97
	Old growth	18.61 (0.71)	0.22 (0.01)	0.97
Mammals	Clearcut	11.82 (0.42)	0.24 (0.01)	0.95
	Young	12.93 (0.33)	0.20 (0.01)	0.96
	Mature	15.10 (0.27)	0.18 (0.01)	0.97
	Old growth	14.14 (0.16)	0.16 (0.01)	0.96

^a $S = CA^z$, where S was number of species and A is number of sites in sample. A varied from 1 to 20, 37, 56, or 53 in clearcuts, young, mature, or old growth, respectively.

See table 1 for description of age-classes.

^c Birds were not sampled in clearcut stands.

Table J-Results of analyses testing equality of nonlinear regression lines relating species richness to numbers of sites in different age-classes of Douglas-fir forests, northwestern California (see fig. 3)

Group	F-ratio	df	P
Amphibians	25.46	6,156	<0.001
Reptiles	223.56	6,156	<0.001
Breeding birds	96.48	4,130	<0.001
Wintering birds	3.21	4,130	<0.010
Mammals	103.91	6,156	<0.001

Inspection of the species-area curves (fig. 3) showed that 20 to 25 sites were required to include at least 90 percent of all species sampled in any age-class. Given a z-value (equivalent to slope coefficient) of about 0.25 (average from table 2), 10 sites would be expected to include about 79 percent and 67 percent of the species that would be expected in 25 and 50 sites, respectively.

Species Similarity

How did species composition differ among age-classes? Species similarity (Jaccard coefficients) averaged 42 percent for amphibians, 37 percent for reptiles, 60 percent for breeding

birds, 54 percent for wintering birds, and 44 percent for mammals between randomly drawn pairs of sites, regardless of age-class. Mean similarity between sites within age-classes and between age-classes was strikingly similar within species groups, especially considering the wide confidence intervals about each mean (fig. 5). Pairs of sites within age-classes were just as likely to share species as pairs of sites between age-classes.

As in analyses of species richness, Jaccard's measure of species similarity was sensitive to the presence of rare species. Therefore, examining similarity based on larger subsets of sites to offset the influence of rare species had more meaning. As larger numbers of sites were included in samples, between-age-class similarity increased for each species group (fig. 6). At larger sample sizes, regression curves predicted nearly equal similarity values among age comparisons for breeding birds, wintering birds, and amphibians. Similarity of reptilian faunas between age-classes tended to converge at sample sizes >10 sites. Similarity of mammalian fauna was consistently lower in clearcut vs. older age-class comparisons than in other comparisons (fig. 6). Bootstrapped estimates of mean similarity, however, had large standard errors, and none of the between-class comparisons could be considered statistically significant, as is evident when 95-percent confidence intervals are plotted around mean values, illustrated for samples of 10 sites (fig. 7).

Discussion

Species richness (alpha diversity) of birds and amphibians did not vary significantly among age-classes of Douglas-fir forest, especially when the effects of rare species were reduced by pooling sites. Reptilian species richness did vary; more species occurred in younger than in older stands. Slightly more mammalian species were found in older than in younger stands.

Total species diversity did not vary much between age-classes. Species similarity (beta diversity) did not vary significantly for any species group, whether comparing sites within age-classes or sites among age-classes. These observations of similar alpha and beta diversities among age-classes led to a conclusion that as area (number of sites) increased, species accumulated at nearly the same rate regardless of age-class. In other words, landscapes composed entirely of clearcuts, old-growth, young forest, or any combination of ages would support similar numbers of vertebrate species. I demonstrated this for amphibians, reptiles, and mammals that I sampled in all four age-classes by comparing species accumulation curves derived for each age-class with the curve derived by randomly drawing sites without regard to age-class (fig. 8). At $n = 10$ sites, mean species richness (\pm 95-percent C.I., experimentwise) varied

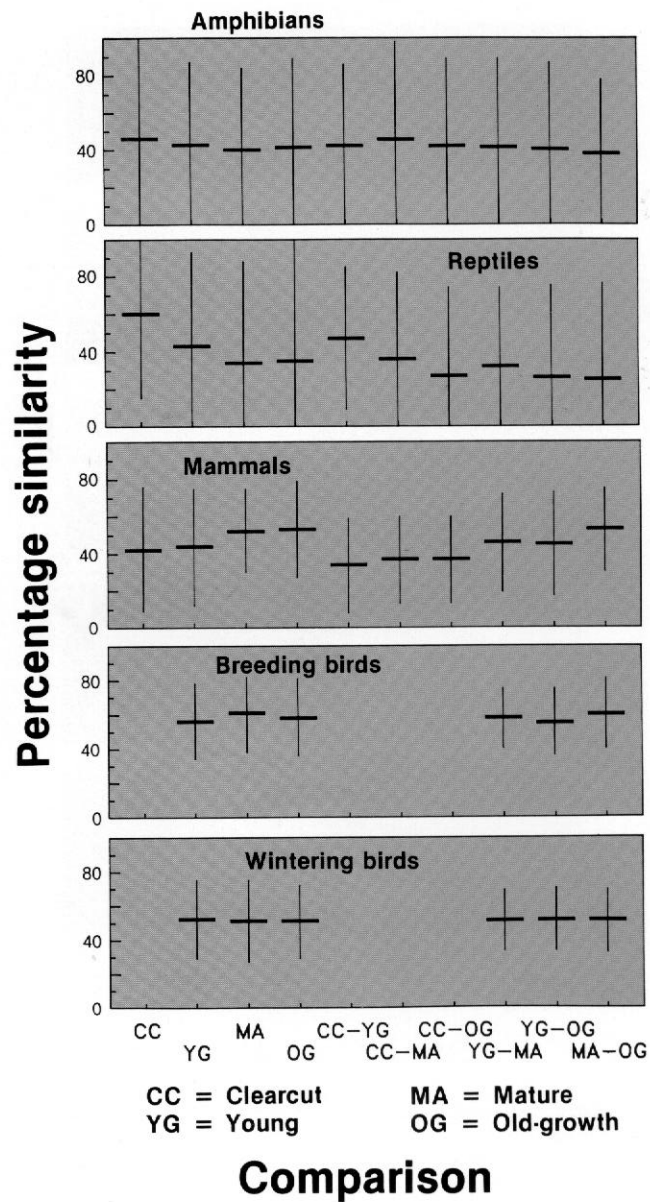
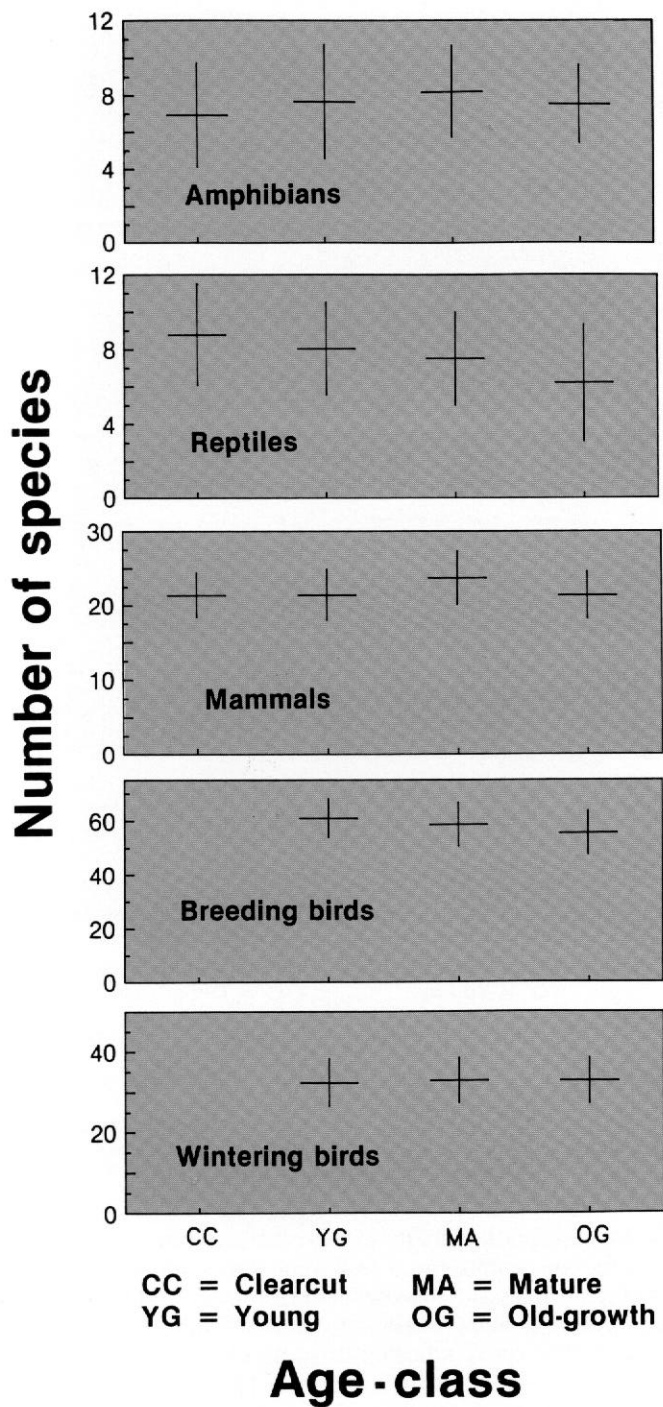


Figure 5—Jaccard similarity (percentage co-occurrence) of amphibian, reptilian, mammalian, and avian species detected at pairs of sites randomly drawn from each age-class (see fig. 1 for codes) or between single sites randomly drawn from different age-classes. Horizontal lines indicate mean similarity from 200 bootstrapped replications; vertical lines indicate 95-percent confidence intervals about the means.

Figure 4—Comparisons of mean species richness (\pm 95-percent confidence intervals) estimated from randomly drawn subsets of 10 sites in each of four age-classes of Douglas-fir forest, northwestern California.

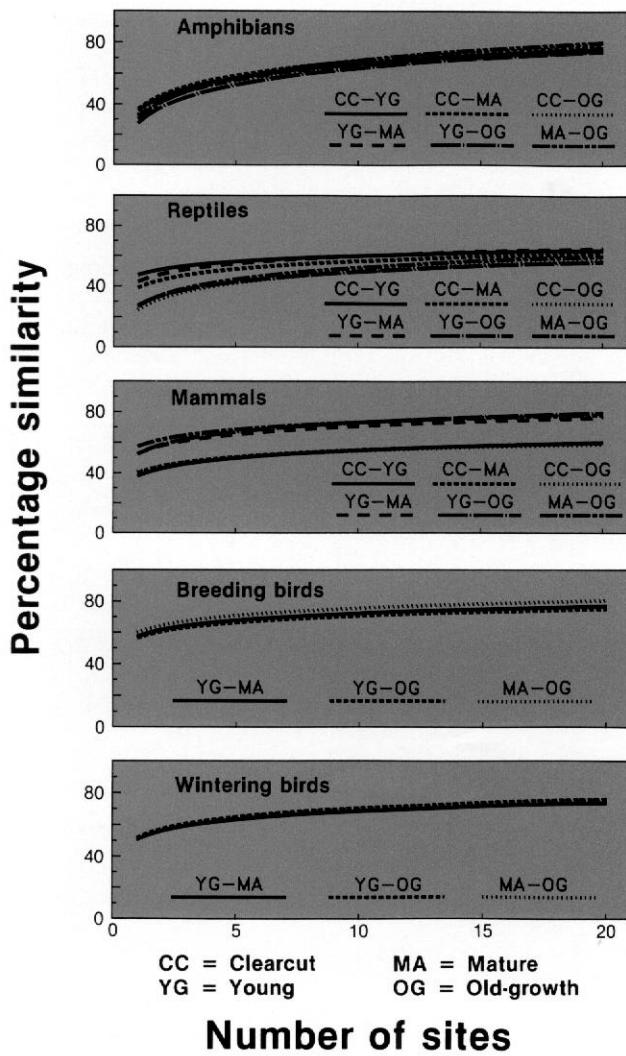


Figure 6—Relation between similarity and numbers of sites for all comparisons between age-classes for each group. Lines are curves fitted to mean similarity calculated for successively larger subsets of sites (up to $n = 20$) by use of a bootstrap procedure.

from 32 ± 8.2 (age-class 1) to 40 ± 9.2 (all age-classes). Thus, confidence intervals overlapped means for all comparisons, indicating insufficient evidence that means differed significantly.

Do these results suggest that all old growth could be eliminated without negative effects on biodiversity? The answer is yes, but only if the number of species is all that counts. As shown elsewhere in these proceedings and by other analyses of these data (Raphael 1988c, Raphael and others 1988), a substantial proportion of species are significantly more abundant in certain age-classes. Loss of preferred age-classes may

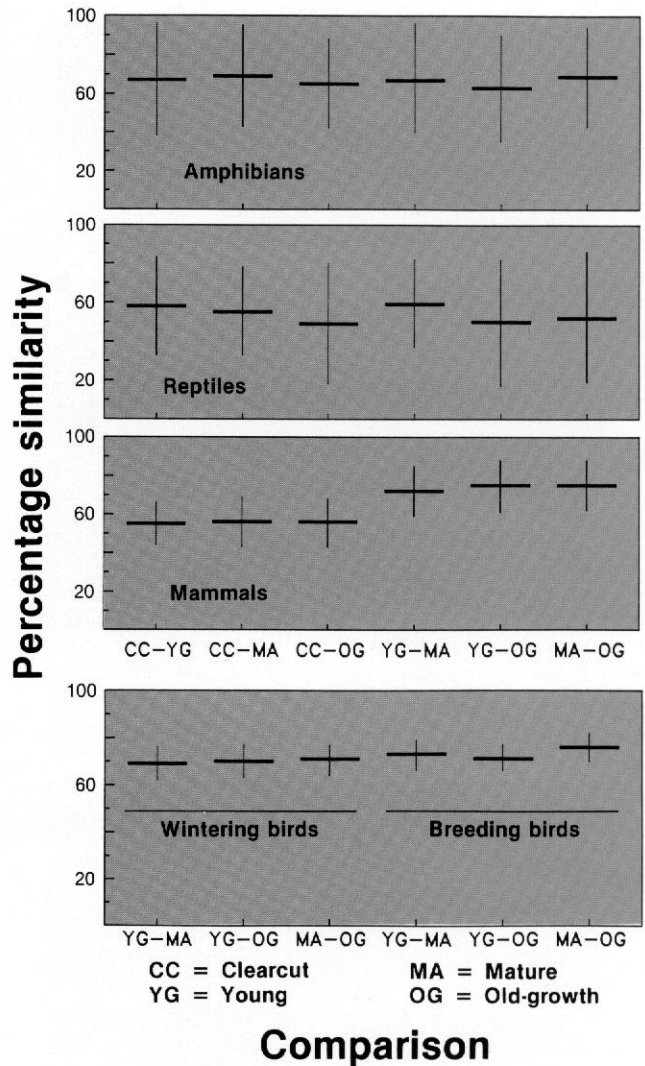


Figure 7—Comparisons of mean similarity (± 95 -percent confidence intervals) estimated from 200 bootstrap replications of 10 randomly selected sites for all possible comparisons between age-classes for each group.

reduce the population viability of these species. Species richness is only one component of biodiversity and, for terrestrial vertebrates of Douglas-fir forests in northwestern California, species richness is not a sensitive indicator of habitat value. Results of my analyses indicate that species richness is independent of age-class, yet other analyses reported in this volume indicate that the abundance of certain species is quite dependent on age-class. For this reason, I agree with conclusions of Samson and Knopf (1982) and suggest that species richness should not be used as a basis for allocating distributions of land base among age-classes. Rather, I suggest that such decisions should be based on more sensitive,

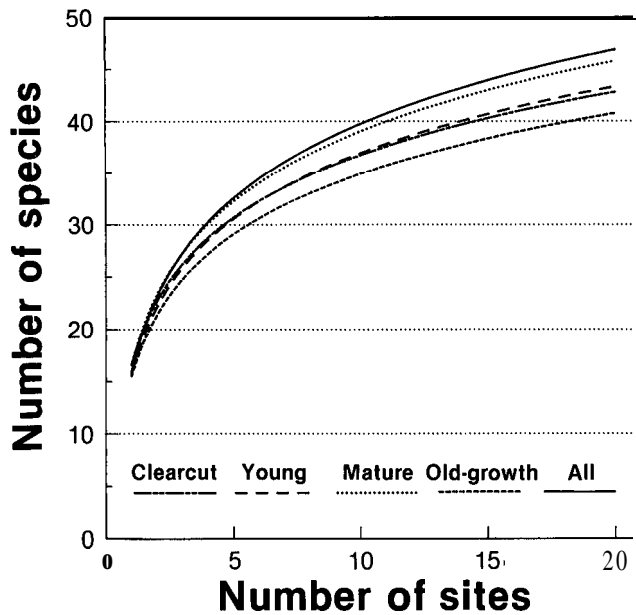


Figure 8—Accumulation of amphibian, reptilian, and mammalian species with increasing numbers of sites for each of four age-classes and for all age-classes combined from Douglas-fir forests of northwestern California.

abundance-based measures. Raphael and Hof (unpubl. data), for example, suggest a MAXMIN approach by use of linear-programming techniques to compute the optimum mix of age-classes to maximize the minimum population sizes of all species of interest. If probabilities of population viability can be maximized, then probabilities of extinction can be minimized and species richness will be maintained.

Acknowledgments

I thank Glen Brink and Marilyn Whitfield for writing bootstrap programs and Rudy King for statistical advice. I also thank my field assistants whose hard work permitted these analyses. Field studies and subsequent analyses were supported by the Pacific Southwest Region and Pacific Southwest Forest and Range Experiment Station of the USDA Forest Service and by the University of California Agricultural Experiment Station, Project 3501 MS. I am indebted to Barry R. Noon and C. John Ralph for comments on earlier drafts.

This paper is contribution 109 of the Wildlife Habitat Relationships in Western Washington and Oregon Research Project, Pacific Northwest Research Station, USDA Forest Service. □

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