

Amphibian Populations in the Terrestrial Environment: Is There Evidence of Declines of Terrestrial Forest Amphibians in Northwestern California?

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ABSTRACT.—Amphibian declines have been documented worldwide; however the vast majority are species associated with aquatic habitats. Information on the status and trends of terrestrial amphibians is almost entirely lacking. Here we use data collected across a 12-yr period (sampling from 1984–86 and from 1993–95) to address the question of whether evidence exists for declines among terrestrial amphibians in northwestern California forests. The majority of amphibians, both species and relative numbers, in these forests are direct-developing salamanders of the family Plethodontidae. We examined amphibian richness and evenness, and the relative abundances of the four most common species of plethodontid salamanders. We examined evidence of differences between years in two ecological provinces (coastal and interior) and across young, mature, and late seral forests and with reference to a moisture gradient from xeric to hydric within late seral forests. We found evidence of declines in species richness across years on late seral mesic stands and in the coastal ecological province, but these differences appeared to be caused by differences in the detection of rarer species, rather than evidence of an overall pattern. We also found differences among specific years in numbers of individuals of the most abundant species, *Ensatina eschscholtzii*, but these differences also failed to reflect a consistent pattern of declines between the two decadal sample periods. Results showing differences in richness, evenness, and relative abundances along both the seral and moisture continua were consistent with previous research. Overall, we found no compelling evidence of a downward trend in terrestrial plethodontid salamanders. We believe that continued monitoring of terrestrial salamander populations is important to understanding mechanisms of population declines in amphibian species.

Declines in amphibian populations have now been documented in many areas around the world (e.g., Alford and Richards, 1999; Houlihan et al., 2000; Stewart et al., 2004; reviewed by Semlitsch 2003). Amphibians in western North America seem to be particularly at risk, especially pond-breeding amphibians (e.g., Drost and Fellers, 1996; Fisher and Shaffer, 1996; Kiesecker et al., 2001; Davidson et al., 2002). The vast majority of these declining western North American species have aquatic larvae; however, a large number of western amphibians are lungless woodland salamanders (family Plethodontidae) that lack aquatic larvae (Petranka, 1998; Stebbins, 2003). All of the western plethodontid genera (*Aneides*, *Batrachoseps*, *Ensatina*, *Hydromantes*, and *Plethodon*) are direct-developing species that hatch as miniature adults from eggs deposited in moist terrestrial substrates (Wake and Hanken, 1996). Hence,

they do not require aquatic environments for reproduction or other aspects of their life histories. Determining whether any of these fully terrestrial species are experiencing declines is a high priority. Welsh and Droege (2001) presented evidence that populations of plethodontid salamanders are remarkably stable over time in undisturbed environments, more so than any other vertebrate group measured. Evidence for declines of plethodontid salamanders would suggest previously undetected perturbations in the environment, with implications for potentially serious negative ecological consequences (e.g., Davic and Welsh 2004).

Plethodontid salamanders in the eastern United States exhibit at least three demographic patterns: (1) long-term stability (Hairston and Wiley, 1993); (2) fluctuations that result in no obvious pattern of decline or increase over time (Pechmann and Wilbur, 1994); and (3) recent (post-1980s) declines (Highton, 2005). Similar assessments have not been conducted on west-

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ern plethodontids. Our study was designed to determine whether terrestrial amphibians in northwestern California exhibit the same patterns seen in eastern plethodontids and, in particular, whether there is evidence of recent declines. We investigated these questions by resampling in the mid-1990s (1993–95) a set of 36 forest stands that had previously been sampled in the mid 1980s (1984–86; Welsh and Lind, 1988, 1991). Species richness, evenness, and the relative abundances of common species were compared over this 12-yr time period.

MATERIALS AND METHODS

Study area.—The sites resampled were a subset of 54 forest stands distributed from Josephine County in southern Oregon to Mendocino County in northern California, which had been sampled in the 1980s by Welsh and Lind (1988, 1991). For logistical reasons, we chose to restrict this study to the 36 stands that were in California (see fig. 1 in Welsh and Lind, 1991). These sites represented a gradient from coast to interior (= two ecological provinces) comprised of 21 coastal and 15 inland sites and covered a forest chronosequence including nine young stands (30–99 years old), nine mature stands (100–199 years old), and 18 late seral stands $\geq$ 200 years old). The late seral stands also represented a moisture continuum from xeric (two stands), to mesic (10 stands), to hydric/wet (six stands) allowing us to simultaneously test for differences in occurrence along a moisture gradient. See Welsh and Lind (1988, 1991) for stand descriptions, stand aging techniques, and moisture assignments. Our intent was to sample all 36 stands in each of the six years. However, six stands were not sampled in 1985, and a single stand was not sampled in each of the years 1993 and 1995. We adjusted for these differences in sampling effort in the statistical design and analysis (see below).

Most of the amphibians in our study had the potential of occurring in all 36 stands, with the exception of the California Slender Salamander (*Batrachoseps attenuatus*), which occurred primarily in the coastal zone, and the Del Norte Salamander (*Plethodon elongatus*), which was distributed primarily in the inland zone. Three interior stands in the Butte Creek drainage were within the range of the California Slender Salamander; and three coastal stands at Hurok Experimental Forest were within the range of the Del Norte Salamander (Stebbins, 2003). Stands were subdivided accordingly for the analyses of these two species (i.e., we did not test ecological province). A total of 24 stands (10 stands for the moisture test) had the potential for California Slender Salamander occurrence,

and 16 (10 stands for the moisture test) had the potential for Del Norte Salamander occurrence (see Welsh and Lind 1988). For the richness and evenness analyses, these two species potentially replaced one another across the set of stands, with the exception of the three Hurok sites where they co-occurred. However both species were rarely encountered at the Hurok sites; thus, we considered their overall influence on richness and evenness to be minimal because they tended to cancel each other out for those metrics.

Amphibian sampling.—We sampled amphibians on each of the 36 stands during the spring in 1984–86. Each stand was sampled on a single day for four person-hours each year using time-constrained searches (TCS; Welsh, 1987; Corn and Bury, 1990). We resampled each stand using the same method from 1993 through 1995. Our TCS method is comparable to the visual encounter survey (VES) described in Heyer et al. (1994). These stands were large (21–150 ha) and it was not possible to examine all potential cover objects on a given stand during any single four-person-hour TCS. The lead author (HHW) conducted all searches in 1984–86 with the assistance of three different but experienced surveyors each year. The 1993–96 searches were conducted by three different teams of two persons, all with prior experience in amphibian sampling, and with each team given additional training by HHW.

We were unable to directly address the issue of potential variation in detectability (e.g., MacKenzie et al., 2003) of our focal species (Plethodontid salamanders; see Hyde and Simons, 2001) because we conducted only one TCS per site each year. However, by focusing our sampling in the spring when surface moisture was high, and western plethodontid salamanders are most active on and near the surface (e.g., Olson 1999), we believe that variation in detectability had a minimal effect on our results. Support for just such a minimum effect came from pitfall trapping, which occurred on most of the same sites during the fall of 1984 and 1985 and rarely yielded new detections of any of our focal species where they had not been previously detected using TCS (Welsh, unpub. data).

Analytical methods.—Our earlier work demonstrated that ecological province, stand age, and moisture influenced amphibian distributions and abundances in this region (Welsh and Lind, 1988, 1991). We included these factors in our current analysis, along with sample year (decade), the main factor of interest. Our hypothesis was that, after accounting for variability caused by these environmental factors, we would be able to detect differences in species

indices over time (one decade) that were the result of longer term factors acting on the populations.

Specifically, we were interested in whether there was evidence for changes in species richness and evenness (Magurran, 1988) and abundance for four species with a relatively high rate of occurrence (*Aneides vagrans*, *B. attenuatus*, *Ensatina eschscholtzii*, *P. elongatus* were detected at >30% of all possible stands by year combinations). These were the response variables. We used a repeated-measures analysis of variance (PROC MIXED; SAS Institute, Inc., Cary, NC, 1997) to test for differences between sets of years (decades) using the mean and standard deviations of years within each decade for each response variable. We also tested for differences between pairs of years within and between decades. Response variables were verified for homogeneity of variances by examining scatter plots of residuals, predicted values, and independent variables. Species count variables were square-root transformed when necessary to achieve normality (e.g., Wandering Salamander, *A. vagrans*; California Slender Salamander, *B. attenuatus*; and Del Norte Salamander, *P. elongatus*). The factors in our models were ecological province (inland or coastal), forest age (young, mature, or old), and year (1984, 1985, 1986, 1993, 1994, and 1995). We tested the null hypothesis of no differences in amphibian numbers between the inland and coastal ecoprovinces, across the forest chronosequence, or as a result of the year of sampling. All possible interactions among these factors were included in the models. Separate models were developed for the subset of old-growth forest stands to examine the effect of stand moisture (wet, mesic, dry) on amphibian numbers. All other factors except forest age were included in these models, but only moisture and interactions between moisture and the other factors were fully explored. The repeated measures analysis used an autoregressive order one covariance structure to account for the length of time between sampling events (years); hence, 1985 was assumed to be more correlated to 1986 than to 1995.

Least-squares means (also called adjusted means) were used because they provide more appropriate estimates in unbalanced designs (i.e., unequal number of stands within each factor; Milliken and Johnson, 1984). When an individual factor was significant (α level of $P < 0.10$; Schrader-Frechette and McCoy, 1993), we conducted pairwise (Scheffe) tests to determine which level component(s) of the factor (e.g., young vs. mature vs. late-seral) differed at $\alpha < 0.10$. By using Scheffe's test we maintained an overall alpha level of 0.10 for all tests. When

interactions were significant, we examined simple effects for one factor within the levels of the other (called the dominant factor) at the appropriate α level (i.e., α was set by dividing 0.10 by the number of pairwise tests performed for each interaction). The selection of the dominant factor in the simple effects analyses was based on our determination of the most interesting question (e.g., for a significant ecological province-decade interaction, we were more interested in the potential differences between the means of the years 1984–86 and the years 1993–96 within ecological provinces than between ecological provinces within individual years).

Post-hoc power analysis.—We used the Mixed Model Procedure in SAS (W. W. Stroup, Cary, NC, 1990) to evaluate the ability of our study design to detect changes in richness, evenness, and individual species numbers. Data from the 1980s were used to determine initial means and standard deviations for richness, evenness, and abundance of four common species. For each species or species metric, power analyses were conducted separately for the full set of stands and for the subset of late seral stands. In each analysis, appropriate covariates were included (i.e., age/ecoprovince for the full set and moisture/ecoprovince for the reduced set). Using this information, we could determine whether resampling the 36 stands in the 1990s would allow us to detect population change between the two distinct time periods (1980s vs. 1990s; with a two-tailed test, changes could be either increases or decreases). The significance level was set at $\alpha = 0.10$, which is recommended for testing ecological differences (Schrader-Frechette and McCoy, 1993). Our goal was to be able to detect an increase or decrease in abundance of ~25% between the mean of the 1984, 1985, and 1986 populations and the mean of the 1993, 1994, and 1995 populations represented by our samples, with power >80%. We believed that a 25% change over a decade would be biologically significant even for an erratic-breeding amphibian (see Pechmann et al., 1991) and would be worthy of further investigation as to possible causes. For example, a 25% decline over the period of our study would translate to an annual decrease of 2.08%.

RESULTS

During the six years of sampling, we detected a total of 5,923 amphibians of 13 species, 2,974 individuals in the 1980s and 2,949 individuals in the 1990s (Table 1). Salamanders of the family Plethodontidae comprised 96.6% of the total sample. Mean values for each dependent vari-

TABLE 1. Amphibians detected with time-constrained searches of 36 forest stands in northwestern California based on six years of sampling. Asterisks indicate plethodontid species.

Species	1984	1985	1986	1993	1994	1995	TOTAL
Tailed Frog	0	2	0	0	0	0	2
<i>Ascaphus truei</i>							
Western Toad	0	0	0	0	1	0	1
<i>Bufo boreas</i>							
Pacific Tree Frog	7	15	22	8	12	14	78
<i>Pseudacris regilla</i>							
Red-Legged Frog	0	0	0	0	1	1	2
<i>Rana aurora</i>							
Northwestern Salamander	1	0	0	2	1	3	7
<i>Ambystoma gracile</i>							
Coastal Giant Salamander	4	7	1	1	6	6	25
<i>Dicamptodon tenebrosus</i>							
Black Salamander*	8	16	11	1	0	15	51
<i>Aneides flavipunctatus</i>							
Wandering Salamander*	63	80	80	75	70	52	420
<i>Aneides vagrans</i>							
California Slender Salamander*	341	290	341	315	405	550	2,242
<i>Batrachoseps attenuatus</i>							
Ensatina*	520	404	452	186	374	484	2,420
<i>Ensatina eschscholtzii</i>							
Del Norte Salamander*	77	88	65	54	112	190	586
<i>Plethodon elongatus</i>							
Southern Torrent Salamander	0	30	1	0	1	0	32
<i>Rhyacotriton variegatus</i>							
Rough-Skinned Newt	11	16	21	4	3	2	57
<i>Taricha granulosa</i>							
TOTAL	1,032	948	994	646	986	1,317	5,923

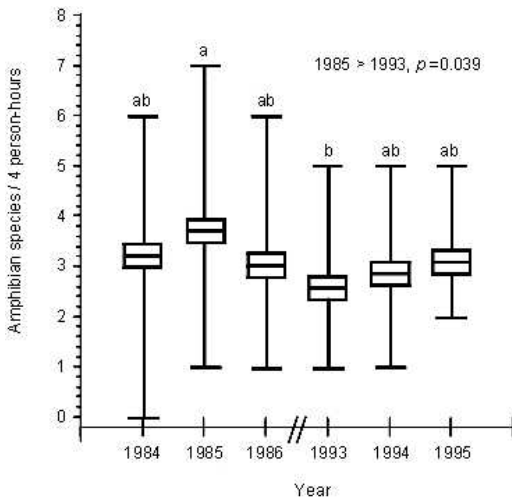


FIG. 1. Amphibian richness by sample year for both ecoprovinces. Effect sizes depicted are least-square means (center lines), $\pm$ SE (boxes), with minimum and maximums (whiskers). Significant differences are indicated by differing letters between pairs.

able (assemblage metric or species) are reported for each independent factor in Table 2.

Amphibian species richness.—Year was a significant factor for two of the six years, with richness higher in 1985 than in 1993 ($P = 0.039$; Fig. 1) but with no significant difference in richness between decades. Neither forest age class nor ecological province alone had a significant influence on species richness, but there was a significant interaction between the two. Within the coastal province, there were more species found on mature and late seral than young stands (Table 3). In the inland province, there were more species found on young than mature stands (Table 3). There was no significant interaction between year and stand age, but there was a significant interaction between year and ecological province, such that within the coastal province, 1985 and 1986 both yielded more species than were detected in 1993 (Table 3). In the inland province, there were also significant differences among years, with more species detected in 1985 than in 1986 (Table 3).

Moisture had a significant effect on species richness with higher richness on mesic stands than on either the wet or dry stands ($P = 0.043$ and $P = 0.065$, respectively). We also found a significant interaction between moisture and

TABLE 2. Means (SE) used with ANOVA to examine amphibian differences (A) among forest age class, ecoprovinces, and years in mesic stands and (B) among ecoprovinces, years, and moisture classes in old-growth stands.

(A) Dependent variable	Forest age			Ecoprovince		Year							
	Young	Mature	Old-growth	Coastal	Inland	1984				1985			
						1984	1985	1986	1987	1988	1989	1990	1991
Richness	3.31 (0.26)	2.84 (0.17)	3.10 (0.12)	3.24 (0.11)	2.93 (0.19)	3.22 (0.23)	3.71 (0.23)	3.04 (0.24)	2.59 (0.23)	2.86 (0.23)	3.10 (0.23)	3.10 (0.23)	3.10 (0.23)
Evenness	0.67 (0.06)	0.54 (0.04)	0.63 (0.03)	0.64 (0.03)	0.58 (0.04)	0.59 (0.05)	0.64 (0.05)	0.60 (0.06)	0.64 (0.06)	0.62 (0.05)	0.57 (0.06)	0.57 (0.06)	0.57 (0.06)
<i>Ensatina escholtzii</i>	13.81 (2.59)	10.90 (1.64)	12.70 (1.16)	8.36 (1.10)	16.58 (1.89)	16.47 (1.90)	13.01 (1.90)	13.90 (1.96)	5.78 (1.90)	11.18 (1.90)	14.47 (1.90)	14.47 (1.90)	14.47 (1.90)
<i>Plethodon elongatus</i>	0.37 (0.52)	0.03 (0.33)	0.99 (0.23)	0.02 (0.22)	0.90 (0.38)	0.49 (0.31)	0.29 (0.31)	0.31 (0.31)	0.25 (0.31)	0.98 (0.31)	0.48 (0.31)	0.48 (0.31)	0.48 (0.31)
<i>Aneides vagrans</i>	0.67 (0.29)	0.80 (0.19)	1.13 (0.13)	0.93 (0.12)	0.80 (0.21)	0.74 (0.22)	1.18 (0.22)	0.92 (0.23)	0.70 (0.22)	0.76 (0.22)	0.90 (0.22)	0.90 (0.22)	0.90 (0.22)
<i>Batrachoseps attenuatus</i>	1.33 (0.44)	2.68 (0.28)	2.16 (0.20)	4.01 (0.19)	0.11 (0.32)	1.89 (0.28)	1.80 (0.28)	2.07 (0.29)	1.93 (0.28)	2.10 (0.28)	2.55 (0.28)	2.55 (0.28)	2.55 (0.28)

(B) Dependent variable	Ecoprovince			Year								Moisture	
	Coastal	Inland	Old-growth	1984				1985				Wet	Dry
				1984	1985	1986	1987	1988	1989	1990	1991		
Richness	3.09 (0.18)	2.80 (0.17)	2.68 (0.26)	3.03 (0.26)	3.08 (0.27)	3.08 (0.27)	2.88 (0.27)	2.89 (0.26)	3.11 (0.26)	2.80 (0.18)	3.45 (0.14)	2.58 (0.30)	2.58 (0.30)
Evenness	0.55 (0.04)	0.66 (0.04)	0.59 (0.06)	0.59 (0.06)	0.56 (0.07)	0.56 (0.07)	0.75 (0.07)	0.58 (0.06)	0.56 (0.06)	0.63 (0.04)	0.66 (0.03)	0.52 (0.07)	0.52 (0.07)
<i>Ensatina escholtzii</i>	11.34 (2.35)	15.89 (2.28)	15.60 (2.85)	11.94 (2.85)	17.15 (2.93)	17.15 (2.93)	4.67 (2.90)	14.25 (2.85)	18.07 (2.85)	9.12 (2.31)	13.88 (1.81)	17.83 (3.94)	17.83 (3.94)
<i>Plethodon elongatus</i>	0.00 (0.69)	1.78 (0.67)	0.74 (0.63)	0.61 (0.63)	0.86 (0.64)	0.86 (0.64)	0.69 (0.63)	1.25 (0.63)	1.20 (0.63)	1.00 (0.67)	1.03 (0.53)	0.64 (1.16)	0.64 (1.16)
<i>Aneides vagrans</i>	0.61 (0.17)	1.36 (0.16)	0.87 (0.27)	1.20 (0.27)	0.81 (0.28)	0.81 (0.28)	1.00 (0.27)	1.01 (0.27)	1.02 (0.27)	0.99 (0.17)	1.39 (0.13)	0.57 (0.28)	0.57 (0.28)
<i>Batrachoseps attenuatus</i>	3.50 (0.17)	0.02 (0.16)	1.70 (0.20)	1.32 (0.20)	1.93 (0.21)	1.93 (0.21)	1.61 (0.20)	1.75 (0.20)	2.25 (0.20)	2.18 (0.16)	2.53 (0.13)	0.57 (0.28)	0.57 (0.28)

TABLE 3. Results of ANOVA analyses of amphibian assemblage metrics (C = coastal, I = inland, Y = young, Ma = mature, L = late seral, W = wet, Me = mesic, D = dry). All tests results are evaluated at an alpha level of <0.10. For simple effects the first level test is an *F*-test and subsequent pairwise results are evaluated by a *t*-statistic with the alpha adjusted for the number of tests (age or moisture within another factor—alpha = 0.033; year within another factor—alpha = 0.0067). * = interaction. †Degrees of freedom are presented as (numerator degrees of freedom, denominator degrees of freedom).

Dependent variable	Factor	Main effects			Simple effects			
		dft	F	P	Result	dft	F/t	P
Richness	Forest age	2, 30	1.39	0.265	—	—	—	—
	Ecoprovince	1, 30	2.07	0.161	—	—	—	—
	Ecoprovince*Age	2, 30	7.23	0.003	Age w/in coastal	2, 30	4.48	0.020
					Ma > Y	30	2.50	0.020
					L > Y	30	2.59	0.015
					Age w/in inland	2, 30	4.86	0.015
					Y > Ma	30	2.99	0.006
	Year	5, 142	2.68	0.024	—	—	—	—
	Forest age*Year	10, 142	0.69	0.729	—	—	—	—
	Ecoprovince*Year	5, 142	2.35	0.044	Year w/in coastal	5, 142	3.13	0.010
					85 > 93	142	3.26	0.001
					86 > 93	142	3.38	0.001
					Year w/in inland	5, 142	2.30	0.048
					85 > 86	142	2.89	0.005
	Age*Ecoprovince*Year	10, 142	0.88	0.556	—	—	—	—
Evenness	Moisture	2, 12	6.04	0.015	—	—	—	—
	Ecoprovince*Moisture	2, 12	7.90	0.007	Mois. w/in coastal	2, 12	12.73	0.001
					Me > W	12	4.19	0.001
					Me > D	12	3.88	0.002
	Moisture*Year	10, 56	2.19	0.032	Year w/in mesic	5, 56	4.06	0.003
					85 > 84	56	3.45	0.001
					85 > 93	56	3.41	0.001
					85 > 94	56	3.92	< 0.001
	Ecoprovince*Moisture*Year	10, 56	1.10	0.382	—	—	—	—
	Age	2, 30	2.38	0.110	—	—	—	—
	Ecoprovince	1, 30	1.18	0.286	—	—	—	—
	Ecoprovince*Age	2, 30	2.65	0.087	Age w/in coastal	2, 30	2.77	0.079
					No sign. pairwise	—	—	—
					Age w/in inland	2, 30	3.90	0.003
					L > Ma	30	2.79	0.009
	Year	5, 142	0.36	0.877	—	—	—	—
	Age*Year	10, 142	0.92	0.513	—	—	—	—
	Ecoprovince*Year	5, 142	1.65	0.152	—	—	—	—
	Ecoprovince*Moisture	2, 12	0.58	0.576	—	—	—	—
	Moisture*Year	10, 56	1.46	0.181	—	—	—	—
	Ecoprovince*Moisture*Year	10, 56	1.13	0.358	—	—	—	—

TABLE 4. Time period estimates, differences, and estimated power to detect differences. Units are mean counts except for the two species where a square-root transformation was performed. Power is evaluated for a two-tailed test at a significance level of 10%.

Dependent variable	Time period		Difference in time periods				Estimated power to detect	
	1984 to 1986	1993 to 1995	Estimate	SE	Lower 90% CL	Upper 90% CL	25% decline	50% decline
Evenness	0.609	0.614	0.004	0.052	-0.082	0.091	0.925	1.000
Richness	3.321	2.849	-0.472	0.222	-0.842	-0.102	0.974	1.000
<i>Aneides vagrans</i>	0.948	0.786	-0.162	0.246	-0.572	0.249	0.300	0.718
<i>Ensatina eschscholtzii</i>	14.460	10.479	-3.981	2.164	-7.592	0.369	0.463	0.928
<i>Plethodon elongatus</i> (square root transformed)	0.736	1.045	0.309	0.698	-0.858	1.476	0.124	0.194
<i>Batrachoseps attenuatus</i> (square root transformed)	1.921	2.194	0.273	0.338	-0.288	0.834	0.488	0.943

ecological province for species richness. Within the coastal province, mesic stands had higher richness than either hydric or xeric stands (Table 3). No such differences were found in the inland province (Table 3). There was also a significant difference in richness based on the interaction between moisture and year, with mesic stands showing higher richness in 1985 compared with 1984, 1993, and 1994 (Table 3). No year differences for species richness were found for wet or dry stands.

Amphibian species evenness.—The only significant difference we detected in amphibian evenness was in the interaction between forest age and ecological province. Within the inland province, late seral stands had higher evenness than mature stands (Table 3). There were no significant pairwise differences among age classes within coastal stands (Table 3).

We met our objective of sufficient power (>80%) to detect a ~25% decline in both amphibian richness and evenness (Table 4). Our power analysis indicated that we could detect a 30% decline in richness (Fig. 2A,B) or evenness (Fig. 2C,D) between the 1980s and the 1990s; for both the forest age/ecoprovince and moisture/ecoprovince models. However, to detect a 10% decline between the 1980s and 1990s, our power would drop to about 0.30.

Individual species.—Of the 5,923 individual amphibians detected, 5,719 (96.6%) were plethodontid salamanders (Table 1). One hundred twenty-one individuals representing four other salamander families accounted for 2.0% of the total. Eighty-three individuals, representing four families of anurans accounted for the remaining 1.4%. Four of the five species of plethodontid salamanders were found in sufficient numbers to examine differences in numbers among sample years, ecological provinces, stand ages, and stand moisture classes (Tables 1,5).

Aneides vagrans.—We captured 420 wandering salamanders (Table 1) but found no differences across years or decades, among age classes, or between ecological provinces (Table 5). We did find a significant interaction between forest age and ecological province, such that within the inland province, captures in late seral were greater than those on mature stands (Tables 2,5). We also found a significant interaction between ecological province and year, with both the coastal and the inland provinces demonstrating differences; however, after adjusting for the number of tests, there were no significant pairwise interactions (Table 5). Captures of *A. vagrans* differed by moisture class, with mesic stands having more captures than dry stands ($P = 0.065$).

Batrachoseps attenuatus.—This species occurs primarily along the coast in northern California (Stebbins, 2003); hence, only the 21 coastal stands, and three stands at Butte Creek, Humboldt County, were used in our analyses ($N = 24$, i.e., no ecological province factor was tested). We captured 2,242 slender salamanders (Table 1). We found no effect for stand age or moisture class, but year was significant with more captures in 1995 than 1993 ($P = 0.064$); however, no decadal differences were observed (Table 5). We also found a significant pairwise interaction between year and mature stands with 1995 having more captures than 1994 (Table 5).

Ensatina eschscholtzii.—This was the most common amphibian encountered, with 2,420 detections (Table 1). We found significant differences between years, with 1984 higher than 1993 ($P = 0.009$), and 1995 higher than 1993 ($P = 0.012$; Table 5, Fig. 3), but no significant difference was found between decades. There were also more *E. eschscholtzii* on inland stands compared with those in the coastal province ($P < 0.001$).

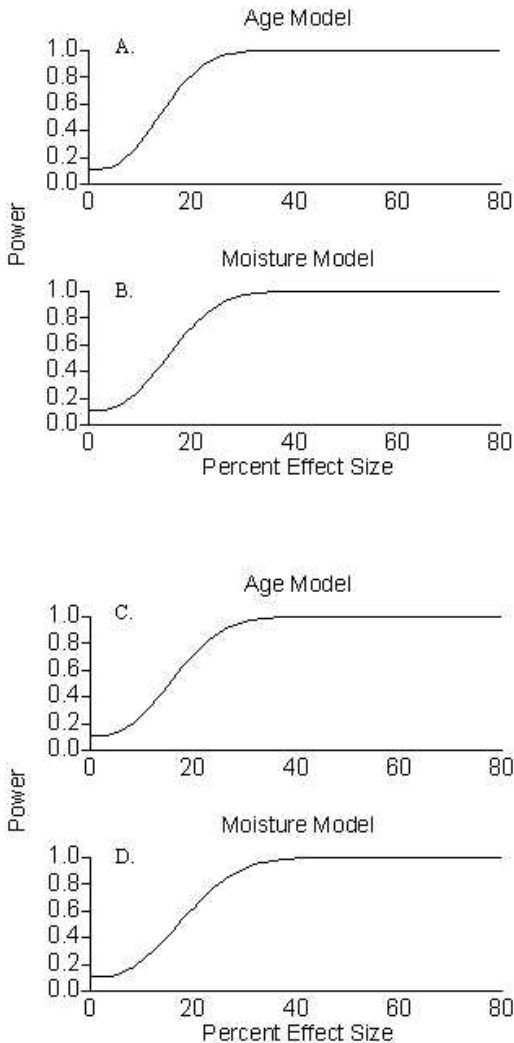


FIG. 2. Power to detect a change between the 1980s and the 1990s for two models of richness—all stands forest age/ecoprovince (A) and late seral moisture/ecoprovince (B); and two models of evenness—all stands forest age/ecoprovince (C) and late seral moisture/ecoprovince (D); with α set at 0.10.

Plethodon elongatus.—This species occurs primarily inland and north of the Mad River in northwestern California except near the Klamath River and north where it ranges to the coast (Stebbins, 2003). Therefore, the analyses of this species covered primarily inland stands north of the Mad River, plus three coastal stands in the Hurok Experimental Forest, north of the Klamath River ($N = 16$; i.e., no test of ecological province). We captured 586 Del Norte Salamanders (Table 1). Tests for the effects of forest age, year, decade, and moisture on

numbers of this species detected all proved to be nonsignificant, as were all tests for interactions (Table 5).

Other salamanders.—Of the four other salamander species that were not evaluated in our ANOVA analysis because of small sample sizes, two appeared to show lower abundances in 1993–95 than in 1984–86 (*Rhyacotriton variegatus* and *Taricha granulosa*), and two appeared to show no differences in detections between the two sets of years (*Aneides flavipunctatus* and *Dicamptodon tenebrosus*; Table 1).

For individual species, our power to detect trends was low, and consequently any effect would have to be large ($\geq 50\%$) to discern a real increase or decrease (Table 4). For *E. eschscholtzii*, the effect for the age/ecoprovince model would have to approach a 40% increase or decrease to achieve power of 70% (Fig. 4A), and for the moisture/ecoprovince model a 40% increase or decrease would have power of only 50% (Fig. 4B). For *A. vagrans*, power was similar, with a 50% change having power of only 60% for both the age/ecoprovince and the moisture/ecoprovince models (Fig. 4C,D). Our ability to detect trends for either *B. attenuatus* or *P. elongatus* was even more limited (Table 3).

DISCUSSION

Our study was designed to evaluate whether there were biologically significant differences in the number of amphibians, especially woodland salamanders, at 36 terrestrial sites sampled in 1984–86 and again in 1993–95. Although we observed significant variation between years for some species and indices, we found no significant declines between the two decadal survey periods (Tables 3, 5). Previous reports of declining amphibians have focused mostly on aquatic breeding anurans (see citations in introduction). This probably reflects the more conspicuous nature of anuran breeding aggregations and the greater challenge of sampling terrestrial amphibians (e.g., Hyde and Simons, 2001). Nonetheless, woodland salamanders of the family Plethodontidae make up 60% of all salamander species worldwide and 96.6% of the amphibians we detected in Northwestern California, suggesting a significant ecological role in these forest ecosystems (e.g., Davic and Welsh, 2004). Hence, with increasingly strong evidence that amphibians worldwide are declining (Stewart et al., 2004; but see Crochet et al., 2004), evaluating the status of terrestrial amphibians, especially woodland salamanders, can aid our understanding of the scope and nature of declines, and help us focus on the most likely cause or causes (Collins and Storfer, 2003). Hairston and Wiley (1993) found no evidence

of a decline in plethodontid salamanders in the southern Appalachians, but Snyder (1991) reported declines in Green Salamanders (*Aneides aeneus*) in Tennessee, and Corser (2001) reported declines of Green Salamanders in North Carolina. Two studies in Central America (Parra-Olea et al., 1999; Lips and Donnelly, 2005) also noted declines in plethodontid salamander populations. The most extensive evaluation of the status of plethodontid salamanders was conducted by Highton (2005). He analyzed data for 44 species of *Plethodon* in the eastern and central United States collected over nearly 50 years (1951 to 1999). He concluded that there was little change in abundance prior to 1985, but beginning in the mid-1980s, he began to observe declines. In the 1990s, he found significant declines when he resurveyed 205 sites with 38 species of *Plethodon*. The mean number observed/person/visit in the 1990s was only 41.6% of that in earlier surveys.

Collins and Storfer (2003) list six leading, but not mutually exclusive, hypotheses to explain amphibian declines, sorting them into two classes. Their Class I hypotheses (i.e., alien species, overexploitation, and land use changes) are causes where we have a good understanding of the ecological mechanisms underlying the declines. Their Class II hypotheses (i.e., global change [including UV radiation and global climate change], contaminants, and emerging infectious diseases) are those where we have a poor, but improving, understanding of how each might cause declines (Collins and Storfer, 2003). Declines in amphibian populations in the western United States have been attributed to each of these factors. However, the factors that may be important in amphibian population declines elsewhere in California (e.g., airborne contaminants, nonnative predators, disease [e.g., Knapp and Matthews, 2000; Fellers et al., 2001; Davidson et al., 2002; Welsh et al., 2006]) are unlikely to be playing a role in the low to midelevation forests in northwestern California. Here the prevailing winds come directly off the Pacific Ocean (i.e., not across major agricultural areas), and there are no known nonnative predators of terrestrial salamanders. Other factors, such as disease, UV-B, and extensive habitat destruction, are also not likely issues for our study region (but see Welsh, 1990). No evidence of recent disease has emerged, UV-B would be blocked by the forest canopy, and the habitats on our particular stands have not been altered since prior to the 1984–86 sampling.

Our finding that amphibian species richness was higher for some years in the 1980s versus some years in the 1990s, overall and in the coastal province (Table 3) is of interest. However, causes for these differences in species

composition are not likely because of a decadal decline because no differences were found for the other years in the 1990s. Furthermore, the total number of species detected in 1984–85 was 11, whereas the total number detected in 1993–95 was 12 (Table 1). One possible explanation for these minor differences in amphibian richness between years is that there have been successional changes between 1984–86 and 1993–95. However, although our earlier work (Welsh and Lind, 1988, 1991) demonstrated higher numbers of plethodontid salamanders in later seral forests, these recent successional changes appear to be insufficient to cause a shift in species composition. Both a lag effect resulting from earlier habitat changes (e.g., Tilman et al., 1994), or climate change at a broader scale (Kiesecker et al., 2001), are also possible explanations for changes in species composition. Although we lack data sufficient to evaluate either of these hypotheses, we believe a more parsimonious explanation is that these differences in richness are caused by variation in the detection of rarer species among years (see Table 1). For example, differences could have been caused by the presence or absence of a few, mostly aquatic or semiaquatic species (Tailed Frog, Northern Red-Legged Frog, Western Toad, and Northwestern Salamander) that, even though we encountered some terrestrial life stages, are better detected using different sampling methods designed specifically for aquatic amphibians. Consequently, we are hopeful that the small differences we found in amphibian species richness do not reflect any real or significant changes in species composition.

Our surveys detected very few differences between sets of years, and failed to detect any patterns across multiple sets of years, for individual species of salamanders. The total number of animals captured during the 1980s was only 25 more than the number captured in the 1990s (2,974 vs. 2,949; Table 1). If we restrict the comparison to the five plethodontid salamanders, the total for the three years in the 1980s is 41 animals less than the number captured in the three years in the 1990s (2,836 vs. 2,883; Table 1). Examining the common species individually revealed no trends. Thus, we did not detect consistent differences among years, or sets of years (1983–85 vs. 1993–95), that might indicate a trend over time, either up or down, for any of the species of plethodontid salamanders we tested (Table 5; c.f. Highton, 2005).

The higher richness and evenness we found relative to both forest stand age (the seral continuum), and stand moisture regime, were consistent with earlier results (Welsh and Lind, 1988; 1991) and with the patterns of richness

TABLE 5. Results of ANOVA analyses of salamander species (C = coastal, I = inland, Y = young, Ma = mature, L = late seral, W = wet, Me = mesic, D = dry). All tests results are evaluated at an alpha level of <0.10. For simple effects the first level test is an *F*-test and subsequent pairwise results are evaluated by a *t*-statistic with the alpha adjusted for the number of tests (age or moisture within another factor—alpha = 0.033; year within another factor—alpha = 0.0067). * = interaction. †Degrees of freedom are presented as (numerator degrees of freedom, denominator degrees of freedom).

Dependent variable	Factor	Main effects			Simple effects		
		df†	<i>F</i>	<i>P</i>	Result	df†	<i>F/t</i> <i>P</i>
<i>Aneides vagrans</i> (square root trans.)	Age	2, 30	1.69	0.201	—	—	—
	Ecoprovince	1, 30	0.29	0.595	—	—	—
	Ecoprovince*Age	2, 30	3.01	0.065	Age w/in inland L > Ma	2, 30	3.87 0.032
	Year	5, 142	1.11	0.360	—	30	2.33 0.027
	Age*Year	10, 142	0.36	0.963	—	—	—
	Ecoprovince*Year	5, 142	4.32	0.001	Year w/in coastal No sign. pairwise	5, 142	2.35 0.044
	Age*Ecoprovince*Year	10, 142	0.93	0.506	Year w/in inland No sign. pairwise	5, 142	2.83 0.018
	Moisture	2, 12	4.22	0.041	—	—	—
	Ecoprovince*Moisture	2, 12	2.46	0.128	—	—	—
	Moisture*Year	10, 56	0.38	0.951	—	—	—
<i>Batrachoseps attenuatus</i> (square root trans.)	Ecoprovince*Moisture*Year	10, 56	0.55	0.845	—	—	—
	Age	2, 21	2.39	0.116	—	—	—
	Year	5, 97	3.54	0.006	—	—	—
	Age*Year	10, 97	2.29	0.018	Year w/in late seral No sign. pairwise	5, 97	3.27 0.009
	Moisture	2, 7	0.83	0.475	Year within mature 95 > 94	5, 97	2.83 0.020
	Moisture*Year	10, 31	1.14	0.364	Year within young No sign. pairwise	97	2.87 0.005
	Age	2, 30	0.59	0.559	—	5, 97	2.59 0.031
	Ecoprovince	1, 30	14.13	0.001	—	—	—
	Ecoprovince*Age	2, 30	0.39	0.683	—	—	—
	Year	5, 142	4.79	< 0.001	—	—	—
<i>Ensatina eschscholtzii</i>	Age*Year	10, 142	1.27	0.252	—	—	—
	Ecoprovince*Year	5, 142	1.31	0.263	—	—	—
	Age*Ecoprovince*Year	10, 142	0.71	0.716	—	—	—
	Moisture	2, 12	2.26	0.147	—	—	—
	Ecoprovince*Moisture	2, 12	0.80	0.472	—	—	—
	Moisture*Year	10, 56	0.84	0.593	—	—	—
	Ecoprovince*Moisture*Year	10, 56	0.73	0.690	—	—	—
	Age	2, 30	0.59	0.559	—	—	—
	Ecoprovince	1, 30	14.13	0.001	—	—	—
	Ecoprovince*Age	2, 30	0.39	0.683	—	—	—

TABLE 5. Continued.

Dependent variable	Factor	Main effects			Simple effects		
		df†	F	P	Result	df†	P
<i>Plethodon elongatus</i> (square root trans.)	Age	2, 13	2.57	0.115			
	Year	5, 60	1.20	0.322			
	Age*Year	10, 60	0.74	0.683			
	Moisture	2, 7	0.33	0.732			
	Moisture*Year	10, 32	0.75	0.673			

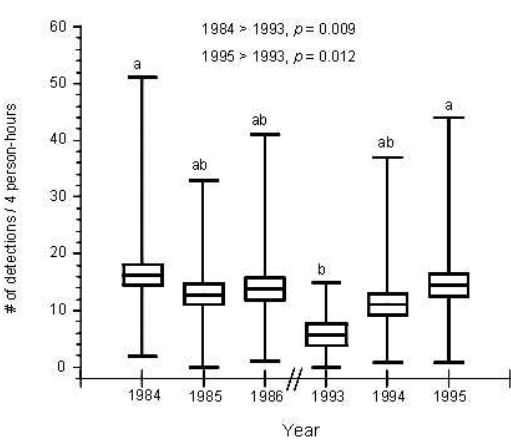


FIG. 3. Detections of *Ensatina* by year. Effect sizes and significant differences indicated as in Figure 1.

and evenness reported for the greater Pacific Northwest (Blaustein et al., 1995), where both late seral and mesic stands, respectively, tend to support the highest richness and evenness of amphibians. Results for individual species were significant for these same factors, and tended to follow the same patterns of more individuals in later seral stages, and in the stands with intermediate moisture regimes (Table 2).

Amphibian population numbers can change dramatically between years, even in pristine environments, making it difficult to distinguish natural fluctuations from declines that might be attributable to some “unnatural” environmental perturbation (Pechmann et al., 1991; Pechmann and Wilbur, 1994). However, Hairston (1987) provides evidence that plethodontid salamander populations, unlike pond-breeding amphibians, do not fluctuate markedly over time, and are quite stable in areas where habitats have not been dramatically altered. Welsh and Droege (2001) presented additional data in support of plethodontid population stability, listing it as one of the advantages for using woodland salamanders for monitoring status and change in forest ecosystems. They compared 35 plethodontid time-series studies of three years duration or greater and found a mean coefficient of variation (CV) of 38.5% (Welsh and Droege, 2001: Table 1). This mean CV was lower than other amphibians and lower than mean CVs reported for passerine birds (57%); small mammals (69%); and lepidoptera (93%; Gibbs et al., 1998). The practical result of low variation in counts is high power to determine the actual abundance across plots or through time. Statistical power in this context is “...the probability that a monitoring program will detect a trend in sample counts when the trend is occurring,

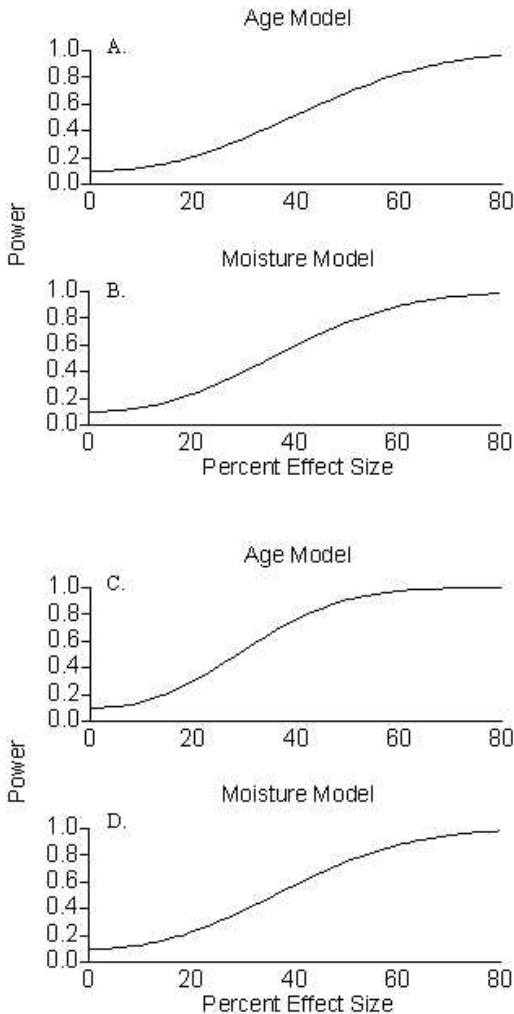


FIG. 4. Power to detect change between the 1980s and 1990s using two models for *ensatina*—all stand forest age/ecoprovince (A) and late seral moisture/ecoprovince (B); and two models for the wandering salamander—all stands forest age/ecoprovince (C) and late seral moisture/ecoprovince (D), with alpha set at 0.10.

despite the noise in the count data..." (Gibbs et al., 1998:935). Analysis of the power of our study design indicated that we could detect a 30% difference in both species richness and total amphibian abundance between the 1980s sample years and those of the 1990s, for both forest age/ecoprovince and moisture/ecoprovince models, with full power (Table 4; Fig. 2). However, for individual species, our power was relatively low and consequently a population change would have to be much greater to be detected (e.g., Fig. 4; Table 4) or the sampling effort increased.

Sampling across two ecoprovinces, three forest age classes, and three moisture classes undoubtedly weakened our ability to detect small changes in either direction, in any one of these sampling categories. A simplified design with a single age and moisture class (i.e., stands of unharvested late seral forest with a mesic moisture regime) would remove the known effects of reduced numbers of plethodontids in earlier seral stages and wet and dry moisture classes. In addition, increasing the number of sites would improve our ability to detect small but real changes should they exist. Finally, we would recommend sampling every year, for a decade, to better explore and control for any real small annual variation in salamanders that might exist at these sites. Declines of species without a clear cause are reasons for concern (Collins and Storfer, 2003). It is important that research on declining amphibians include species that lack aquatic larvae, especially now that there is increasingly strong evidence for population declines, not only in woodland salamanders, but also in terrestrial frogs (Stewart, 1995; Lips, 1999). Furthermore, new evidence of chytrid fungus in terrestrial salamanders (Cummer et al., 2005) is also cause for vigilance. Consequently, it appears that tracking changes in plethodontid salamander abundances over time has merit and is worthy of continuing efforts.

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