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ACIDIC DEPOSITION AS AN UNLIKELY CAUSE FOR AMPHIBIAN POPULATION DECLINES IN THE SIERRA NEVADA, CALIFORNIA

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Abstract

*The Sierra Nevada of California is one of many regions worldwide that has recently experienced dramatic declines in amphibian populations. During the past two to three decades many populations of at least two species (*Rana muscosa *and* Bufo canorus*) have disappeared in national parks and designated wilderness areas at high elevation, whereas populations of a third widespread species (*Pseudacris regilla*) have remained stable or declined to a lesser extent. Acidification from atmospheric deposition has been suggested as a cause for these disappearances primarily because most surface waters in these areas are exceptionally low in acid neutralizing capacity (ANC), and thus are vulnerable to changes in water chemistry due to acidic deposition. We tested the hypothesis that acidification of habitats has adversely affected amphibian populations by eliminating populations from waters most vulnerable to acidification, i.e. low in pH or ANC, or from waters low in ionic strength, a condition that increases the sensitivity of amphibians to low pH. A survey of 235 potential breeding sites in 30 randomly selected survey areas failed to reveal significant differences in water chemistry parameters between sites with and sites without each of the three species. Moreover, the water chemistry parameters did not differ among sites inhabited by the three species in a manner paralleling their degrees of acid tolerance. These findings contraindicate acidic deposition as a cause of recent amphibian population declines in the Sierra Nevada at high elevation.*

Keywords: acidic deposition, amphibians, Sierra Nevada, pH, *Rana muscosa, Bufo canorus, Pseudacris regilla.*

INTRODUCTION

During the past two to three decades, amphibian populations have disappeared or declined in numbers in many parts of the world, often for unknown reasons (Barinaga, 1990; Wake, 1991). These declines have been particularly conspicuous in some montane regions, including areas that appear to have been minimally impacted by human activities (Wake & Morowitz, 1990). One such region is the Sierra Nevada of California and Nevada at high elevation (Jones and Stokes Associates, 1987; Blaustein & Wake, 1990; Wake, 1991). Here, numerous populations of at least two of the five aquatic-breeding amphibians have been affected. These are the mountain yellow-legged frog *Rana muscosa* and Yosemite toad *Bufo canorus*, both historically widely distributed at high elevation (*c.* >2000 m; Zweifel, 1955; Karlstrom, 1962; Blaustein & Wake, 1990; Bradford, 1991; Bradford *et al.*, in press; D. L. Martin, pers. comm.). Many populations have disappeared from

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seemingly pristine environments, including areas within Sequoia, Kings Canyon, and Yosemite National Parks, and several designated wilderness areas. These disappearances appear to represent true extinctions rather than temporary patterns resulting from limited population monitoring (Pechmann *et al.*, 1991) because populations have not recovered from disappearances that occurred between 10 and 30 years ago (Bradford *et al.*, in press).

In contrast, populations of a third widespread species, the Pacific tree frog *Pseudacris* (*=Hyla*) *regilla*, are much more common at high elevation than populations of the above two species (this study), and appear to be either non-declining (Cooper *et al.*, 1988; Bradford *et al.*, in press) or declining much less dramatically than the other two species (G. M. Fellers, D. L. Martin, pers. comm.). The status of the remaining two aquatic-breeding species at high elevation, western toad *Bufo boreas*, and long-toed salamander *Ambystoma macrodactylum*, is largely unknown (M. R. Jennings, pers. comm.).

Acidification of amphibian breeding waters by atmospheric deposition has been suggested as a cause for amphibian population declines in several areas, including mountains in the western US (Harte & Hoffman, 1989, 1994; Blaustein & Wake, 1990; Wyman, 1990; Carey, 1993). For the salamander *Ambystoma tigrinum* in a high-elevation watershed in the Rocky Mountains, Harte and Hoffman (1989, 1994) provide evidence that acidic deposition is 'a possible anthropogenic cause for occasional failure of salamander recruitment'. Others, however, argue that several recent studies do not support the acidic deposition hypothesis as a causal factor for the widespread population declines of several amphibian species in the Rocky Mountain region, including population fluctuations of *A. tigrinum* (Corn *et al.*, 1989; Corn & Vertucci, 1992; Vertucci & Corn, 1994). In the Sierra Nevada at high elevation because surface waters typically are extremely low in acid neutralizing capacity (ANC), generally more so than in the Rocky Mountains, and thus are vulnerable to changes in water chemistry due to acidic deposition (Landers *et al.*, 1987; Eilers *et al.*, 1989; Melack & Stoddard, 1991). Episodes of reduced pH typically occur during snowmelt and summer storms (Melack & Stoddard, 1991; Williams & Melack, 1991), which coincide with the occurrence of embryonic and larval stages of these species. The embryo is the amphibian life stage generally most sensitive to reduced pH, whereas the larva is generally the most sensitive to elevated concentrations of aluminum that often occur as a result of reduced pH (Pierce, 1985; Freda, 1986, 1991). Moreover, the ionic strength of many Sierra Nevada surface waters is among the lowest in the world (Landers *et al.*, 1987), and low ionic strength increases the sensitivity of amphibians to low pH (Freda & Dunson, 1984; Bradford *et al.*, 1992).

Lack of data on the timing of population declines and limited data on water chemistry during potential episodes of acidification (Melack & Stoddard, 1991) prevent us from directly addressing the proposition that acidic deposition has affected amphibians in the Sierra Nevada. However, the hypothesis that acidification has been responsible for declines can be addressed by examining the relationship between remaining populations of amphibians and the water chemistry of breeding waters. If human-induced acidification has adversely affected amphibians, either by itself or in combination with other factors, their populations would be expected to have disappeared primarily from the waters most vulnerable to acidification (i.e. low in pH and ANC). Two specific hypotheses are addressed in this study: (1) extant amphibian populations breed less commonly in waters with low pH, ANC, or electrical conductivity (EC) in comparison to available breeding sites (EC is included because of the potential for ionic strength to influence an amphibian's sensitivity to low pH); (2) the three species examined differ in the water chemistry of their breeding sites in the same manner that they differ in tolerance to acidic conditions. LC_{50} pH values (based on 7 days at experimental pH) for embryos differ significantly in post-hoc pairwise comparisons among the species (LC_{50} pH values in parentheses): *P. regilla* (4.23) < *R. muscosa* (4.37) < *B. canorus* (4.58) (Bradford *et al.*, 1992, unpublished data). LC_{50} pH values for hatchling tadpoles differ significantly between *R. muscosa* and the other two species: *R. muscosa* (<4.0) < *B. canorus* (4.25) < *P. regilla* (4.30) (Bradford *et al.*, 1992, unpublished data). We tested these hypotheses by conducting extensive field surveys for sites containing or lacking these species in randomly selected areas in the Sierra Nevada at high elevation.

METHODS

Thirty survey areas were included in this study. Each consisted of a 15-km^2 circle (diameter = 4.4 km) exclusive of an average of 7% of each circle's area that was below 2440 m elevation. The center of each circle was randomly selected from a uniform grid established as part of the US Environmental Protection Agency's Environmental Monitoring and Assessment Program with a minimum elevation of 2440 m. The 30 survey areas were divided randomly into two equal subsets, one of which was surveyed in 1990 and the other in 1991. All survey areas were within the known geographic ranges of *P. regilla* and *R. muscosa*, whereas 23 were within the known range of *B. canorus* (Zweifel, 1955; Karlstrom, 1962; Stebbins, 1985).

Two individuals searched each survey area in a manner designed to provide data for sites with each amphibian species and sites lacking the species, and to ascertain whether a breeding population of each species existed within the survey area. Survey areas were searched during the day in early and mid summer (31 May–23 July 1990; 12 June–2 August 1991) when amphibian larvae are most abundant and visible in shallow water near shore (Bradford, 1984). The areas were searched in a non-random manner until five 'different or separate' sites containing larvae (or eggs) of each species were found, or until all suitable breeding habitat had been searched. 'Different or separate' sites were defined as ones more than 200 m apart or that appeared to have disconnected surface water sources (e.g. a pool in a stream versus an isolated pond). Sites were surveyed for amphibian larvae by walking in or near shallow water near shore. Survey areas were also searched in a non-random manner for five 'different or separate' sites that appeared to represent potential breeding habitat for each amphibian species, but which lacked the species. Assessment of potential breeding habitat was based largely on (1) geographic range of each species and elevational limit of 3660 m (Zweifel, 1955; Mullaly & Cunningham, 1956; Karlstrom, 1962); (2) depth or other characteristics suggesting that the time interval during which standing water was available would be sufficient for tadpoles to reach metamorphosis; and (3) absence of predatory fishes unless significant emergent vegetation isolated some areas from fishes (Bradford, 1989).

At each site, an unfiltered water sample was taken in a clean, rinsed 125-ml high-density polypropylene bottle. Some samples were filtered for comparison with unfiltered samples using a 1 μm Nucleopore filter and an all-plastic filter holder and plastic syringe. Approximately 10% of samples were taken as duplicates. Water samples were kept cool and in the dark until analyzed for pH, ANC, and electrical conductivity (EC) at the Sierra Nevada Aquatic Research Laboratory within six days of collection (mean = 2.1 days). Environmental parameters taken at each site were: elevation (derived from 7.5-min USGS topographic maps), water temperature (to 0.1°C, using a thermometer calibrated against a NIST-traceable thermometer), and maximum depth of the water body (estimated visually from shore as one of five categories: <0.50 m, 0.51–1.00 m, 1.01–1.50 m, 1.51–2.0 m, >2.0 m).

Water chemistry values were assumed to represent the relative vulnerability of sites to acidification and potential effects on amphibians (i.e. lowest ANC, pH, or EC) because watersheds with low values for a parameter at a given time of year also tend to have low annual minimum values (Sickman & Melack, 1989; Melack *et al.*, 1991). Moreover, sampling was done during or within a few weeks of peak watershed discharge due to snowmelt.

pH was measured at room temperature using a Fisher Acumet 910 meter (Fisher Scientific, Pittsburgh, PA) or Orion SA250 meter (Orion Research, Boston, MA), and Ross combination electrode (Orion Research, Boston, MA). The electrode was calibrated daily with standard buffers and checked periodically using dilute solutions of HCl (10^{-4} and 10^{-5}N). Acid neutralizing capacity (ANC) was determined by incremental titration with 0.1N HCl (Gran titration; Talling, 1973). Electrical conductivity (EC) was measured with a YSI model 35 conductance meter (Yellow Springs Instruments, Yellow Springs, OH) (cell constant = 0.1 cm) at room temperature.

A comparison of nine filtered versus unfiltered samples revealed no significant differences ($p \gg 0.05$) in pH, EC, and ANC. Fourteen unfiltered duplicate samples differed from each other by averages of 0.1 pH unit and 8.3 μg/litre (ANC) between the two meters ($p<0.001$). However, samples were randomly assigned to each meter for analysis.

Water chemical characteristics were compared between sites containing a breeding species and those considered potential habitat for that species, but lacking the species. Comparisons were made both 'within' and 'between' survey areas. 'Within survey areas' comparisons were made using the ANOVA model (Wilkinson, 1990):

$$\begin{aligned} Y = {} & \text{Constant} + \text{Survey Area} + \\ & \text{Species Presence} + \text{Elevation} + \text{Depth} \qquad (1) \end{aligned}$$

where Y = pH, log ANC, or log EC; Constant = a value generated by the analysis; Survey Area = a category variable representing each survey area containing the species (1, 2, etc.); Species Presence = a category variable for larvae present or absent at a site (0 or 1); and Depth = a category variable as defined above (1, 2,... or 5). Elevation and depth are included in the analysis because the three water chemistry parameters (Y, above) were negatively correlated with elevation within survey areas ($p<0.01$ for each parameter), and log EC differed significantly among depth categories ($p=0.03$). Temperature was omitted because it did not correlate significantly with any of the water chemistry parameters. Wilks' Lambda statistic (Wilkinson, 1990) was computed to test for multivariate effects of pH, log ANC, and log EC. 'Between survey areas' comparisons were made using the following ANOVA model:

$$Y = \text{Constant} + \text{Species Presence} + \text{Elevation} \qquad (2)$$

where Y = mean pH, geometric mean (= mean log) ANC, or geometric mean EC of sites within each survey area; and Species Presence = a category variable for larvae present or absent within the survey area. For survey areas containing a species, sites used to compute means were those containing the species, whereas for survey areas lacking the species, sites used were those considered potential breeding habitat for the species. Depth is omitted from Model 2 because the loss of degrees of freedom in the analysis would be substantial.

In a similar manner, water chemistry was compared among species by replacing 'Species Presence' in Models 1 and 2 with 'Species', where Species = a category variable representing each of the three species. These new models are referred to as Models 3 and 4. The 'within survey areas' 'among species' comparison (Model 3) was limited to pairwise comparisons between *P. regilla* and each of the other two species, because only one survey area contained more than two species. In the analysis of all of the above models, three sites were excluded as statistical outliers (pH<5.0 and/or ANC<0). Sites with such values are extremely rare in the Sierra Nevada (Melack & Stoddard, 1991).

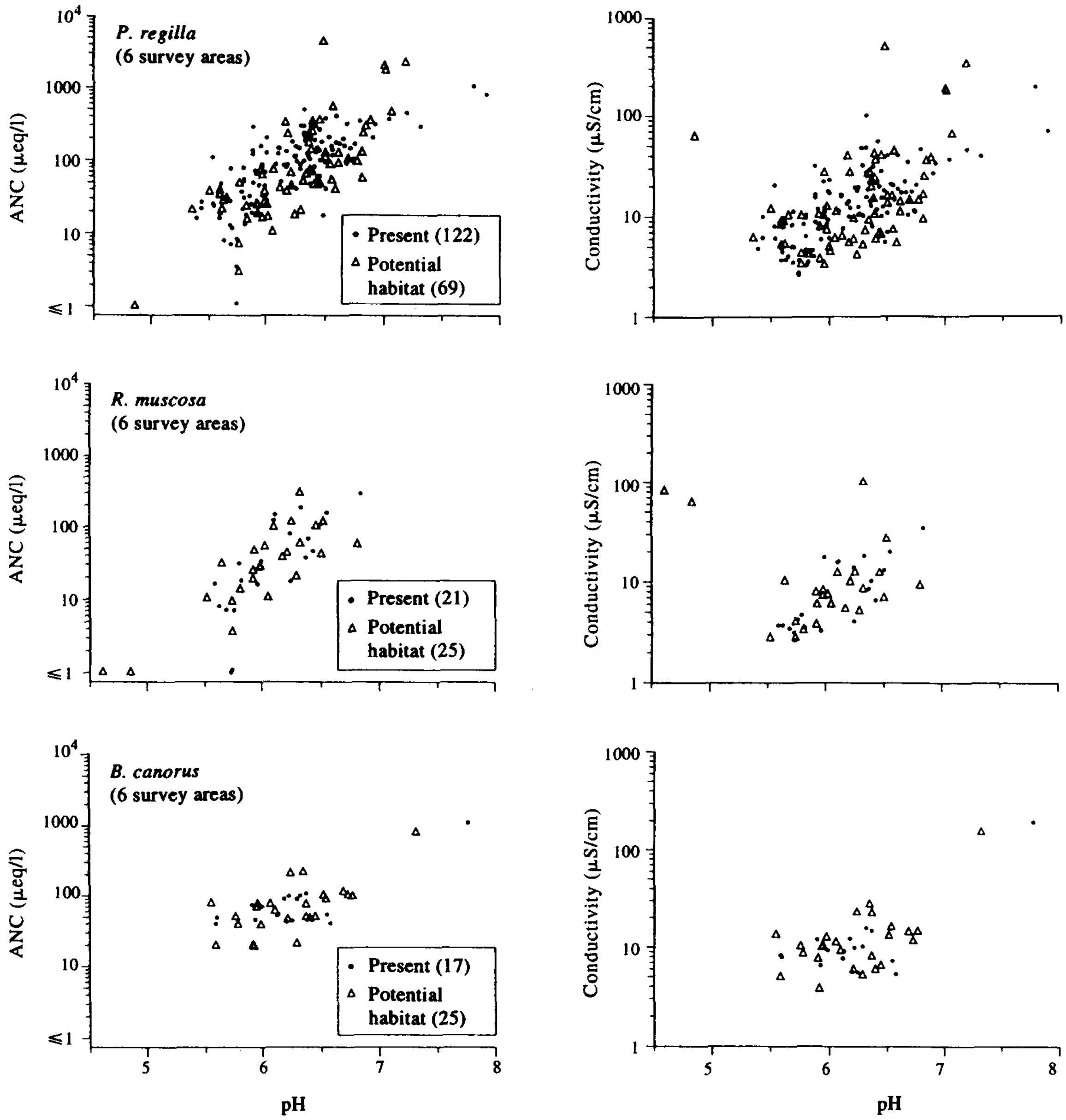

Fig. 1. pH, acid neutralizing capacity (ANC), and electrical conductivity (EC) for sites where breeding amphibians are present and for sites considered potential habitat but lacking the species. Survey areas represented are only those containing the species. Numbers in parentheses represent total number of sites within the survey areas. Three sites shown are excluded from statistical analyses as outliers. Specific values for pH, ANC, and EC at these three sites were, respectively, 4.61, –13.1, 81.2 (site 1); 4.85, 0.1, 62.2 (site 2); and 5.73, –1.5, 3.18 (site 3).

Table 1. Probability values (*p*) for effects of amphibian presence/absence on water chemical parameters: within survey areas (Model 1) and between survey areas (Model 2)

	P. regilla				*R. muscosa*				*B. canorus*			
	'Within'		'Between'		'Within'		'Between'		'Within'		'Between'	
	p	d.f.	*p*	d.f.	*p*	d.f.	*p*	d.f.	*p*	d.f.	*p*	d.f.
pH	0·879	1, 159	0·770	1, 25	0·966	1, 31	0·152	1, 24	0·720	1, 30	0·099	1, 17
log ANC	0·190	1, 159	0·821	1, 25	0·664	1, 31	0·318	1, 24	0·941	1, 30	0·095	1, 17
log EC	0·046	1, 159	0·814	1, 25	0·768	1, 31	0·261	1, 24	0·467	1, 30	0·041	1, 17
Lambda	0·185	3, 157	0·994	3, 23	0·967	3, 29	0·498	3, 22	0·479	3, 28	0·191	3, 15

Lambda is Wilks' Lambda statistic (Wilkinson, 1990) for multivariate effects of species presence/absence on pH, log ANC, and log EC. d.f., degrees of freedom.

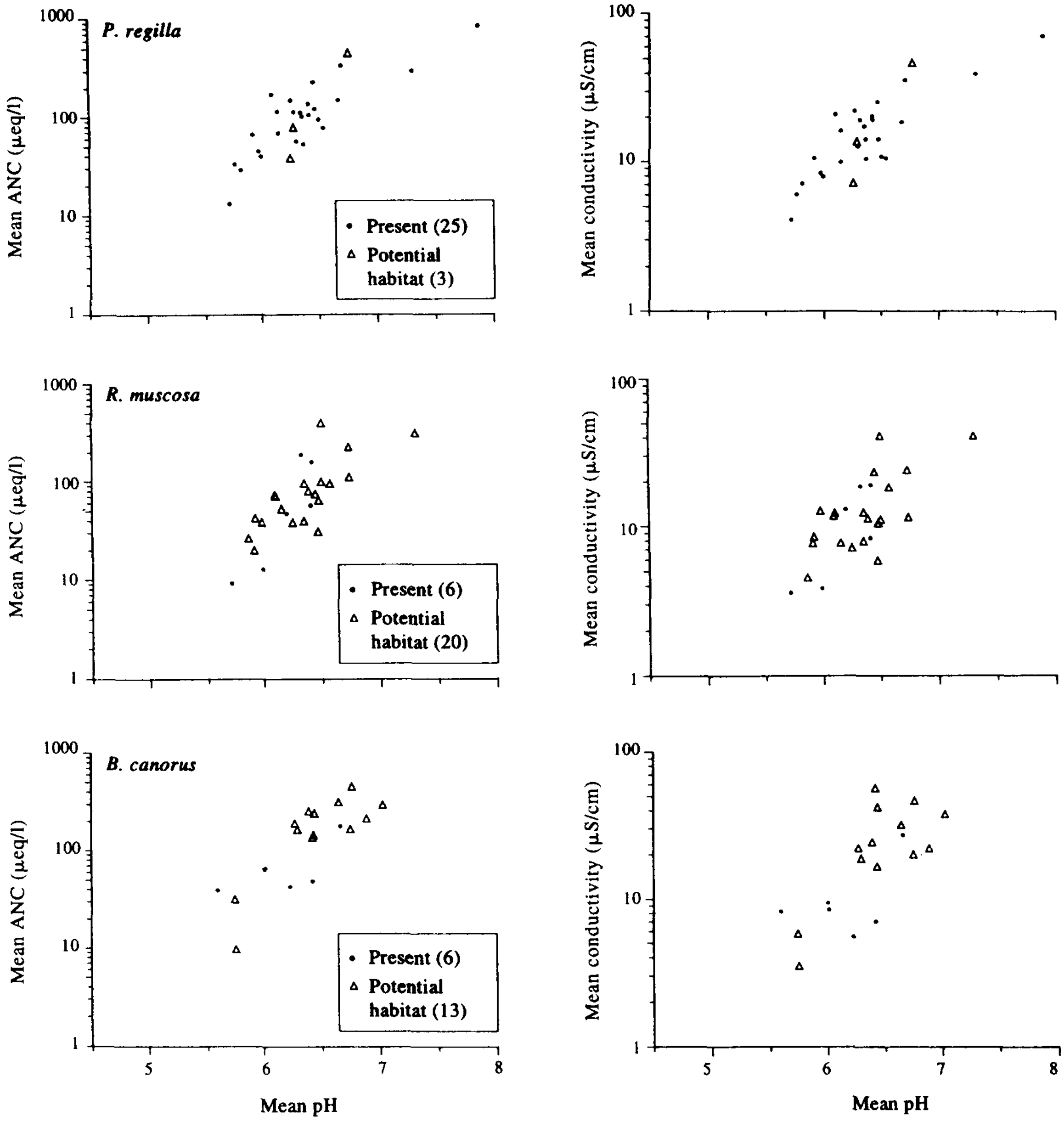

Fig. 2. Mean pH, and geometric means for ANC and electrical conductivity, for survey areas where breeding amphibians are present and for survey areas considered potential habitat but lacking the species. Numbers in parentheses represent number of survey areas. Three sites were excluded from computation of means as described in Fig. 1.

RESULTS

Amphibians were found in 25 of the 30 survey areas. *Pseudacris regilla* was present in all 25, whereas *R. muscosa* and *B. canorus* were each found in six, *B. boreas* in two, and *A. macrodactylum* in one. Two species (*P. regilla* plus another) occurred together in 13 survey areas, and three species (*P. regilla*, *R. muscosa*, and *B. canorus*) occurred together in one.

For each of the three species of concern, water chemistry parameters overlapped considerably between sites containing a species and sites lacking the species (Fig. 1). When analyzed 'within survey areas' according to Model 1, multiple R^2 values were highly significant for all species ($R^2>0.5$ and $p<0.001$ for all species and parameters). However, Wilks' Lambda statistic for multivariate effects of presence/absence on pH, log ANC, and log EC was not significant for any species, and a significant univariate difference for presence/absence was found only for log EC in *P. regilla* ($p=0.046$; Table 1). In this case, EC (untransformed data) was greater for sites lacking *P. regilla* by a factor of 1.20 (based on coefficients derived for Model 1), an effect opposite to

Table 2. Probability values (*p*) for significant differences in water chemistry among species: within survey areas (Model 3) and between survey areas (Model 4) (Lambda and d.f. are defined in Table 1)

	Within survey areas				Between survey areas	
	P. regilla vs *R. muscosa*		*P. regilla* vs *B. canorus*		All species	
	p	d.f.	*p*	d.f.	*p*	d.f.
pH	0·813	1, 42	0·206	1, 33	0·402	2, 33
log ANC	0·516	1, 42	0·443	1, 33	0·115	2, 33
log EC	0·468	1, 42	0·856	1, 33	0·088	2, 33
Lambda	0·899	3, 40	0·333	3, 31	0·285	6, 60

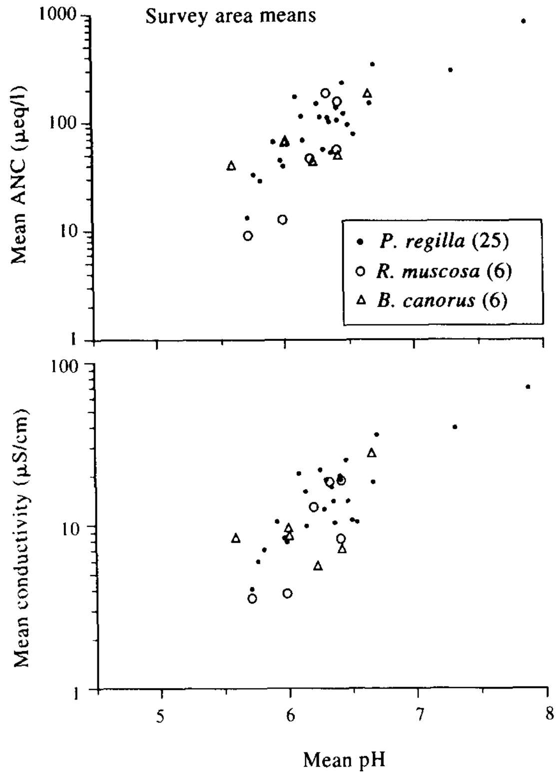

Fig. 3. Mean pH, and geometric means for ANC and electrical conductivity, for survey areas containing each species. Definitions as in Fig. 2.

that predicted in Hypothesis 1. This difference is not evident in Fig. 1 because of pronounced effects on log EC from Survey Area and Elevation found in the analysis of Model 1, which are not represented as variables in the two-dimensional figure.

In the 'between survey areas' comparison of presence/absence (Model 2), Wilks' Lambda was again not significant for any species, and a significant univariate effect for presence/absence was found only for log EC in *B. canorus* (p=0.041; Table 1). In this case, EC (untransformed data) was greater for survey areas lacking *B. canorus* by a factor of 2.27 (based on coefficients derived for Model 2). This effect is evident in Fig. 2 because elevation (which is not represented as a variable in the figure) varied little between sites containing and sites lacking the species. Again, this effect is opposite to that predicted by Hypothesis 1.

In species comparisons 'within survey areas', neither *R. muscosa* nor *B. canorus* sites differed significantly from *P. regilla* sites in pH, log ANC, or log EC (Table 2). In the 'between survey areas' 'among species' comparisons (Fig. 3), the three parameters (pH, log ANC, log EC) did not differ significantly among the species, based both on Wilks' Lambda and univariate statistics (Table 2).

DISCUSSION

Acidic deposition has been an attractive hypothesis to explain amphibian population declines in the Sierra Nevada, in part because it could account for the broad geographic distribution of affected populations, including those near human activities as well as isolated populations in remote locations. However, the present study does not support this hypothesis. For the three species studied, two of which show recent population declines, water chemistry did not differ between sites containing the species and sites lacking the species in a manner consistent with the acidic deposition hypothesis (Hypothesis 1). For *R. muscosa* no significant differences in water chemistry were found. For *P. regilla* and *B. canorus*, the only observed differences (i.e. greater EC for sites or survey areas lacking each species) were opposite to that expected if acidic deposition had eliminated some populations. In a separate study of *P. regilla* in a localized area of Sequoia National Park, pH and ANC did not differ between sites containing the species and sites lacking the species (Soiseth, 1992). Similarly, a species-specific difference in the water chemistry of breeding sites consistent with the acidic deposition hypothesis (Hypothesis 2) is not supported because no significant differences were found in water chemistry among the species.

Other data also contraindicate the acidic deposition hypothesis. Bradford *et al.* (1992) suggested that the lowest pH likely to occur in the surface waters in the Sierra Nevada during episodes of acidification is 5.0. This pH is above the levels known to cause reduced survival of embryos or hatchling tadpoles in any of the three species addressed here, although sublethal effects were observed in *R. muscosa* at pH 5·25. (Bradford *et al.*, 1992, unpublished data).

Recent declines of many amphibian populations around the world may be caused by a multiplicity of factors that vary among species, regions, and time (Barinaga, 1990; Blaustein & Wake, 1990; Wake, 1991). Aside from acidic deposition, pertinent hypotheses for amphibian population declines in the Sierra Nevada include predation by introduced fishes, population fragmentation by such fishes, increased ultraviolet radiation, disease, immunosuppression, livestock grazing, and pesticide contamination (Hayes & Jennings, 1986; Bradford, 1989; Bradford, 1991; Bradford *et al.*, 1993; Carey, 1993). Of these, the hypotheses best substantiated (and most extensively investigated) are those involving introduced fishes and disease. The present study strongly suggests that attention be given to alternative hypotheses rather than acidic deposition. However, investigation of such hypotheses may be difficult because several factors may be operating simultaneously, key causal events may be episodic rather than chronic, and substantial time lags in population responses may exist.

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