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# DECLINES OF THE CALIFORNIA RED-LEGGED FROG: CLIMATE, UV-B, HABITAT, AND PESTICIDES HYPOTHESES

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*Abstract.* The federally threatened California red-legged frog (*Rana aurora draytonii*) has disappeared from much of its range for unknown reasons. We mapped 237 historic locations for the species and determined their current population status. Using a geographic information system (GIS), we determined latitude, elevation, and land use attributes for all sites and analyzed the spatial pattern of declines. We then compared the observed patterns of decline to those predicted by the climate change, UV-B radiation, pesticides, and habitat alteration hypotheses for amphibian decline. Declines were not consistent with the climate change hypothesis but showed a strong positive association with elevation, percentage upwind agricultural land use, and local urbanization. These results apply to patterns of decline across the entire range of *R. a. draytonii* in California, as well as within geographic subregions. The elevational gradient in declines is consistent with the UV-B hypothesis, although the UV-B hypothesis also predicts a north-to-south gradient in declines, which we did not observe. The association of declines with the amount of upwind agricultural land use strongly suggests that wind-borne agrochemicals may be an important factor in declines. This association was most pronounced within the Central Valley–Sierra region, where other studies have documented both transport and deposition of pesticides to the Sierra Nevada and the presence of pesticide residues in the bodies of congeneric (*Rana muscosa*) and more distantly related (*Hyla regilla*) frog species.

*Key words: amphibian decline; California red-legged frog; climate change; declining amphibians; geographic information system (GIS); habitat alteration; pesticides;* Rana aurora draytonii; *spatial analysis; upwind agricultural land use; UV-B; wind-borne agrochemicals.*

## INTRODUCTION

Since they were first brought to the attention of the herpetological and conservation biology communities a decade ago (Barinaga 1990, Wake 1991), amphibian population declines have become a focal issue in both the scientific and popular media (for recent summaries, see Alford and Richards 1999, Corn 2000). Although controversy still persists over the existence, intensity, and optimal ways to document these declines (Shaffer et al. 1998, Alford and Richards 1999), most researchers now agree that many species and some entire communities (Fisher and Shaffer 1996) of amphibians are undergoing ecological collapse. To date, researchers have used observational studies, sometimes combined with historic records, to document declines (Fellers and Drost 1993, Ingram and MacDonald 1993, Drost and Fellers 1996, Fisher and Shaffer 1996, Lips 1998, 1999). At the same time, laboratory studies (Long et al. 1995, Berger et al. 1998), field experiments (Blaustein et al. 1994, Kiesecker and Blaustein 1995, Ovaska et al. 1997, Anzalone et al. 1998, Lawler et al. 1999), and field-based correlational studies (Hayes and Jennings 1988, Bradford 1989, Corn and Vertucci 1992) have been used to elucidate possible causes of declines.

In this study, we develop a two-pronged approach to testing hypotheses for declines. First, we use historic records and recent distributional data to document spatial patterns of decline (Bradford et al. 1993, Jennings and Hayes 1994*a*, Fisher and Shaffer 1996). We then generate predictions of the spatial pattern of declines for competing hypothesized causal mechanisms, and we statistically compare the observed and predicted patterns. The power of this strategy resides in its broad, species-wide approach that avoids reliance on one or a few study sites, as well as the ability to simultaneously evaluate multiple hypotheses for causes of declines. In addition, the analysis of spatial patterns is a powerful and relatively quick method to assess possible causes of decline. The approach takes advantage of the extensive distribution data that already exist in natural history museums and recent surveys (Reznick et al. 1994, Shaffer et al. 1998, Wake 1998), and combines this information with often readily accessible geographic information system (GIS) data on land use, elevation, and other factors.

Like many amphibians in western North America

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(Stebbins and Cohen 1995), the California red-legged frog (*Rana aurora draytonii*) was once abundant (Jennings and Hayes 1985). Today, it is a federally threatened species, which has disappeared from >70% of its historic range in California for unknown reasons (Hayes and Jennings 1986, 1988, Jennings 1988, 1995, 1996, Jennings and Hayes 1994*a, b,* Fisher and Shaffer 1996). A number of local factors, including commercial harvesting (Jennings and Hayes 1985) and habitat alteration due to urbanization, mining, grazing, water diversions, and dams have been suggested as possible causes of declines (Hayes and Jennings 1986, Jennings 1988, 1996, Jennings and Hayes 1994*a, b*). While past commercial harvesting and habitat alteration have certainly contributed to red-legged frog declines, the species has declined from many locations where these issues do not appear to be a factor. In addition, red-legged frogs continue to persist in many areas where habitats have been altered due to grazing, are near urban areas or in localities where commercial harvesting previously reduced populations. In addition to habitat alteration, a number of other factors have been proposed as possible causes of amphibian declines in general, some of which have been suggested specifically for *R. a. draytonii.* Primary among these are the following: (1) climate changes associated with global warming, (2) increases in ultraviolet radiation due to ozone depletion (hereafter referred to as the UV-B hypothesis), (3) airborne contaminants, (4) disease, and (5) introduced exotic fish and bullfrog (*Rana catesbeiana*) predators (for reviews see Corn [1994], Alford and Richards [1999], Corn [2000]). We analyzed the climate change, UV-B, pesticides, and habitat destruction hypotheses, because each has distinct implications for spatial patterns of declines.

The global warming and UV-B hypotheses predict specific patterns of decline associated with changing altitude and latitude. Global warming is expected to shift species ranges poleward and up slope to higher elevations (Peters 1991, Parmesan 1996). Climatic data for 1900–1994 indicate that almost all California state climate divisions show a 3°C/100 yr increase in mean daily temperature, and a 20%/100 yr decrease in mean precipitation (Karl et al. 1996). If global warming were a major contributor to red-legged frog declines, we would expect to see a greater proportion of declines (i.e., a greater proportion of historically present sites are now absent for the species) in southern latitudes, with reduced declines to the north. Similarly, greater declines would be expected at lower altitudes compared to montane sites. Global warming may also affect frogs through changes in precipitation (Pounds and Crump 1994, Laurance 1996, Pounds et al. 1999), in which case we might expect to see proportionately greater declines at drier sites.

Under the UV-B hypothesis, we would expect to find proportionately greater declines both at higher elevations and at more southerly latitudes, where there is greater UV-B exposure (Blumthaler 1993, Cabrera et al. 1995, Madronich et al. 1995, Herman et al. 1999). Based on stratospheric ozone, surface albedo, and cloud cover measurements taken from the Nimbus 7/TOMS satellite during 1979–1992, we estimate that the annual mean human erythema UV-B exposure increased from 0.46% to 0.7% per year along a north–south transect through our study area (calculations from data in S. Madronich, B. Mayer and C. Fisher, *unpublished manuscript*). Although there is a perception that declines have been concentrated at higher elevations (Wake 1991), and thus that UV-B is a potential causal agent, this pattern remains to be quantified for any individual species across an elevational gradient. In addition to increases in UV-B exposure with elevation, in California there is a north-to-south gradient of increasing UV-B exposure (Herman et al. 1999). Therefore, if UV-B were contributing to declines, we would expect to find both increased up-slope declines (opposite the climate change hypothesis) and a north-to-south gradient of declines similar to that predicted by the climate change hypothesis.

If wind-borne pesticides, herbicides, or other agrochemicals were contributing to declines, we would expect to see greater declines at sites that are closer to upwind agriculture, or that have greater amounts of upwind agricultural land use, compared to sites with different land use patterns. California agriculture used $>87 \times 10^6$ kg of pesticide active ingredients in 1995 alone (Department of Pesticide Regulation 1995). A number of studies have documented transport and deposition of pesticides from the Central Valley to the Sierra Nevada (Zabik and Seiber 1993, Aston and Seiber 1997, Datta 1997, McConnell et al. 1998), as well as reporting the presence of pesticide residues in the bodies of other species of congeneric (*Rana muscosa*) and more distantly related (*Hyla regilla*) Sierra frogs (Cory et al. 1970, Datta et al. 1998). However, to date, there has been no direct evidence linking pesticides to amphibian population declines.

Finally, if habitat destruction or modification associated with intensive human activities were contributing to declines, we would expect to see greater declines at sites that have greater amounts of surrounding urban or agricultural land use, compared to sites surrounded by wildlands. Such habitat effects could be due to direct habitat destruction, or they may be more indirect and linked to increased mortality due to automobiles (Fahrig et al. 1995), increases in human-associated predator activity (Crooks and Soulé 1999), or other effects.

Here, we examine the spatial relationship between the distribution of California red-legged frog sites with extant and extirpated populations to quantitatively test the predictions of the climate change, UV-B, pesticide, and habitat destruction hypotheses for red-legged frog declines. Although we cannot address all recently hypothesized reasons for declines (for example, introduced exotic predators or disease), we can use our historical approach to quantitatively test the predicted patterns of decline for four important postulated causes of decline.

## MATERIALS AND METHODS

We compiled California location records for *R. aurora draytonii* primarily from museum records and published literature (Lockington 1879, Grinnell and Storer 1924, Storer 1925, Ingles 1932*a*, *b*, 1933, 1936, Fitch 1949, Neitzel 1965, Cowan 1979, Wernette et al. 1982, Sweet and Leviton 1983). Jennings and Hayes provided additional sites from herpetologists' field notes and sightings used in their *Reptiles and Amphibians of Special Concern in California* (Jennings and Hayes 1994*a*). Locations within 0.8 km of each other were treated as a single site. Multiple location records for a single site were grouped together to determine the earliest observation date. In analyses using historic records, comparisons are often made between attributes of historic sites and the same attributes for recent survey sites. Thus, there are two possible sources of any observed changes: real changes in species distribution that have occurred between the historic and current sampling dates, and differences between the distribution of historic sites and the distribution of recent survey sites. To eliminate this second possible source of changes, we restricted our analysis entirely to historic sites. Sites for which at least one pre-1975 observation existed were deemed ''historic locations,'' and these formed the main data set for statistical analysis. Locations with only observations from 1975 or later were treated as ''nonhistoric'' and only used in a single analysis. Although red-legged frogs have been in decline since the late 1800s due to commercial harvesting (Jennings and Hayes 1985) and habitat destruction (Jennings and Hayes 1994*a*), we chose 1975 as the cutoff year for historic locations, because recent, unexplained declines are believed to have begun sometime in the early 1970s. Because of our interest in analyzing the effects of climate change, UV-B, and pesticides, we decided to only include sites in our main data set where we felt that there was at least some remaining suitable habitat, hence where population status at the site could potentially indicate the impact of these factors. We therefore excluded 26 completely urbanized sites, mostly within the San Francisco, Los Angeles, or San Diego urban areas, where frogs are now absent. However, as part of a robustness analysis, we quantified the effect of deleting these sites on our overall conclusions.

We determined current population status (frogs present or absent) for all sites based primarily on published results of field surveys during 1988–1996 by Mark Jennings and Marc Hayes (Hayes and Jennings 1988, Jennings and Hayes 1994*a*, Jennings 1996) and surveys conducted by the authors in 1997 and 1998. Survey techniques included daytime visual encounter surveys, dipnetting for larvae, and nighttime visual surveys with flashlights. For a few additional sites, population status was assigned based on correspondence with local experts and recent literature. For roughly half of the sites, no direct field observations were available, but the regions were well enough known that we felt that it was appropriate to rely on the judgment of one of us (M. Jennings) to assign site population status, based on known habitat conditions at the site and the presence or absence of red-legged frogs in the immediate vicinity. This technique has been frequently used in large-scale analyses of this type (e.g., Moyle and Randall 1998; Marchetti et al., *in press*) and underlies the geographic approach to planning for biological diversity (GAP) analysis (Scott et al. 1993), which uses animal–habitat relationship models based in large part on expert opinion. We performed a number of statistical analyses to assess the effect of the ''expert opinion'' sites on our overall analysis of declines.

We mapped unique location records using U.S. Geologic Survey (USGS) 1:100 000 scale digital topographic quadrangles and ArcView version 3.0 GIS software, and employed Albers map projections to maximize the accuracy of area measurements (Environmental Systems Research Institute 1992). We derived elevation for all mapped locations using ARC/INFO versions 7.1.1 and 7.2.1 GIS software and USGS 1:250 000-scale digital elevation models for California. Mean annual precipitation spanning 1900–1960 for each site was estimated using a Teale Data Center digital precipitation map of California. Latitude for each location was determined directly from the coordinates for the mapped point. To assess the contribution of habitat destruction to declines, we measured the percentage of urban and agricultural land use in a 2 km radius circle surrounding each site.

To analyze upwind distance to agriculture and amount of upwind agricultural land use, we first estimated predominant wind direction for each site from streamline wind maps for California and wind direction data for 145 wind stations relevant to the range of the red-legged frog (Hayes et al. 1984). Wind direction observations are most often recorded using a compass divided into 16 sectors (e.g., north, north–northeast, northeast, etc.). Predominant wind direction is defined as the midpoint direction of the three contiguous sectors containing the greatest number of observations (Hayes et al. 1984). Based on the regional wind patterns in the San Francisco Bay Area, South Coast, Sacramento, and San Joaquin regions, the predominant summer wind pattern in all regions is also the predominant annual wind direction (Hayes et al. 1984). Therefore, we used the streamline wind map for summer (June–August) to estimate the predominant wind direction for frog sites.

For each red-legged frog site, we analyzed the relationship of the site to agricultural land use within a 33.75° (1.5 compass sectors) wide, 150 km long triangle facing upwind (Fig. 1). We choose 150 km as the length of the triangle, based on biologically relevant

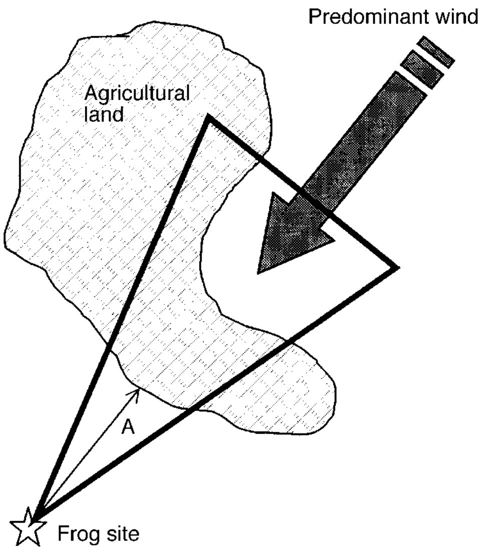

FIG. 1. Illustration of upwind agricultural land use measurements. For each frog site, we drew a 33.75°, 150 km long triangle oriented toward the direction of the prevailing winds. Within the triangle, we measured upwind distance to the nearest agricultural land use (A), and the percentage of the total area of the triangle consisting of agricultural land use.

estimates of possible transport distance for agricultural chemicals in the literature. Cory et al. (1970) and Datta et al. (1998) found agricultural chemicals in the bodies of tadpoles and fish in the Sierra Nevada, ~161 km and ~121 km, respectively, from their likely source in the Central Valley. We analyzed triangles of different widths, ranging 22.5–45° (one to two compass sectors) and found that the different widths did not significantly change the results presented here. Within the upwind triangle, we used USGS digital 1:250 000-scale land use/land cover maps to calculate the percentage of total area in agricultural land use and distance to the nearest agricultural land use from the red-legged frog site at the triangle's vertex (Fig. 1). For sites located within agricultural land use, distance to agriculture was assigned as 0 km. For sites with no agricultural land use within the triangle, distance to agriculture was assigned as 150 km. Measurements of agricultural land use in an upwind triangle might indicate habitat alteration, rather than wind-borne contaminant sources. If this were the case, the percentage of surrounding agricultural land use, but not the directionality with respect to wind (i.e., upwind agricultural land use), should predict frog declines. To test for this possibility, we measured agricultural land use in a triangle the same size as the upwind triangle, but oriented randomly at each site. We also analyzed agricultural land use in a square, 200 km on a side, centered on each site. The 200-km square provided a comparison measurement of agricultural land use at approximately the same distance from each locality as the upwind triangle, but taken in all directions. Although we focus on pesticides, a pattern of declines associated with upwind agricultural land use could be driven by any possibly wind-blown substance that negatively effects frogs (e.g., fertilizer; Marco and Blaustein 1999, Marco et al. 1999), although pesticides seem like the most likely candidate because of their toxicity and documented long-range transport.

For all statistical analyses, we conducted significance tests at the $\alpha = 0.05$ level. For univariate analyses, we used nonparametric Mann-Whitney rank tests to evaluate differences in the mean value of characteristics of sites with present populations and sites with absent populations. Variables with significantly different means were also analyzed as categorical variables and plotted to assess whether there was a consistent quantitative relationship between the proportion of sites with declines and changes in the variable. This is similar to the analysis of a dose–response relationship, and provides an additional and more explicit test of the quantitative relationship between declines and a variable than the simple difference in means between present and absent sites. We used $\chi^2$ tests to evaluate the significance of the relationship between population status and each categorical variable. To assess the possibility of confounding effects due to high colinearity between variables, we calculated Pearson product-moment correlations for all pair-wise combinations of variables. Finally, we used multiple logistic regression to evaluate the multivariate relationship between declines and geographic, precipitation, elevational, and land use variables (Hosmer and Lemeshow 1989). We built a full model with all of the variables, and then removed variables with statistically insignificant coefficients, one by one, to derive a reduced model with only significant variables.

Observed patterns of declines, such as an elevation difference between present and absent sites, might be partially or wholly due to regional differences in declines. For example, if most historic high-elevation sites were in the Sierra Nevada, and for whatever reason there were great declines in the Sierra Nevada but not elsewhere, this would produce a pattern of declines concentrated at high elevations. To control for such potential regional variation, all sites were divided into three regions based on Jepson geographic regions of California (Hickman 1993). A ''Central Valley–Sierra'' region combined the Great Central Valley, Sierra Nevada, Cascade Range, and Northwestern Jepson regions, a ''Southern California'' region consisted of the Southwestern, Sonoran, and Mojave Desert regions, and a ''Central Coast'' region matched the Central Western region. ''Region'' was then treated as a categorical variable and entered in the reduced logistic regression model to check for interactions. If we found no region-by-factor interaction, we interpret this to mean that a factor has a relatively uniform effect across all regions. We also performed separate regression analyses for each region using the same procedures as were used for the statewide model to estimate the effect of each causal factor in each of the three regions.

We performed a number of analyses to assess the reliability of our data and the robustness of our results to possible data errors. To validate both the expert-opinion and direct-observation status determinations, we compared the broad patterns on our map against three other datasets: the California Natural Diversity Data Base (NDDB 1999), a compilation of all U.S. Forest Service amphibian surveys conducted in the Sierra Nevada in the last nine years (Davidson 1999), and intensive surveys in Southern California conducted by Robert Fisher and Ted Case (Fisher and Case, *in press*).

We performed several tests to assess the effect of the expert opinion sites on our overall results. First, we added a new categorical variable for method of site status determination (direct observation or not) to the statewide logistic model, and assessed the significance of interactions between this new variable and the four model variables. Second, we divided the sites into two data sets, based on method of status determination, and analyzed each separately. We calculated mean site characteristics and reran our basic statewide logistic regression model on each set of data, and compared the results between these two datasets, as well as between the direct observation sites and the full data set containing both the direct-observation and expert-opinion sites. To assess the sensitivity of our analyses to errors in site population status in general, we conducted simulations in which population status (that is, frogs present or absent) was switched at 10% and 20% of all sites chosen at random. After switching population status, we reran the statewide logistic model and compared the coefficients and $P$ values to the original model. We repeated each simulation 10 times. To assess the sensitivity of our results to population status errors at a few key sites, we performed traditional outlier analysis of regression residuals using studentized residuals and leverage, Cook's distance, and DFBETA indicators (Neter et al. 1996). All sites that were identified as potentially influential outliers based on these measures were tested in two ways. In one test, we dropped each site from the dataset one at a time, reran the basic statewide regression model, and compared the results to the original model. In a second test, we reran the regression model for each site, but instead of dropping the site, we switched its population status. Finally, we constructed a new categorical variable reflecting our certainty of a site's original historic record (site based on verified museum specimen or not) and used it to test the importance of historic record certainty on our final results.

When analyzing spatial data, there is always the possibility of unwanted spatial autocorrelation (in which nearby sites are not truly independent observations), which may influence statistical analyses (for a review see Legendre [1993]). If this were the case, then the situation would be akin to pseudoreplication, where degrees of freedom are inflated and estimated parameter variances are biased downwards, which may lead to erroneous conclusions concerning statistical significance. To assess this possibility in our data, we ran five simulations in which we randomly removed from our dataset all sites that were $<5$ km from any other site. Telemetry studies on California red-legged frogs have thus far observed maximum travel distances of $<4$ km (J. B. Bulger, *personal communication*), suggesting that sites $\geq 5$ km apart are essentially demographically independent. We also ran simulations with a 10-km minimum separation distance. For each of these simulations, we reran the reduced logistic regression model and examined the coefficients and significance levels.

## RESULTS

We obtained 1520 location records for California red-legged frogs, representing ~659 unique locations. Slightly >80% of the records were from museum specimens, and the remainder were from the literature, field notes, and unpublished sightings. Of the unique locations, 339 had both population status information and sufficiently detailed location descriptions to permit mapping. Of the 339 mapped locations, 237 were based on at least one pre-1975 observation, and these formed the main dataset that we used in our analysis (Fig. 2; see the Appendix). An additional 102 locations were based only on nonhistoric (1975 and later) records. Of the 237 historic red-legged frog sites, 113 (48%) were assigned a current population status of ''absent,'' and 124 (52%) were assigned ''present'' status. Field survey data from Jennings and Hayes (1994*a*), our own surveys, and personal communications with other observers accounted for status determination at 47% of the sites, and expert opinion accounted for the remaining 53%.

### *Univariate analysis of patterns of decline*

Mean values for elevation, percentage upwind agricultural land use, and percentage surrounding urban land use were all significantly higher at sites with absent populations than sites with present populations (Table 1). Mean latitude was significantly to the south for absent sites compared to present sites, and mean percentage agricultural land use in a surrounding 200-km square was significantly higher at present sites than absent sites (although the absolute difference was <2%). Percentage surrounding agricultural land use in a circle with a 2-km radius shows a marginally significant increase for absent sites ($P = 0.023$), which we interpret cautiously given the large number of tests in this analysis. Means for average precipitation, distance to agriculture, upwind distance to agriculture, and percentage agricultural land use in a randomly oriented triangle all showed no significant difference between present and absent sites. There was a significant rela-

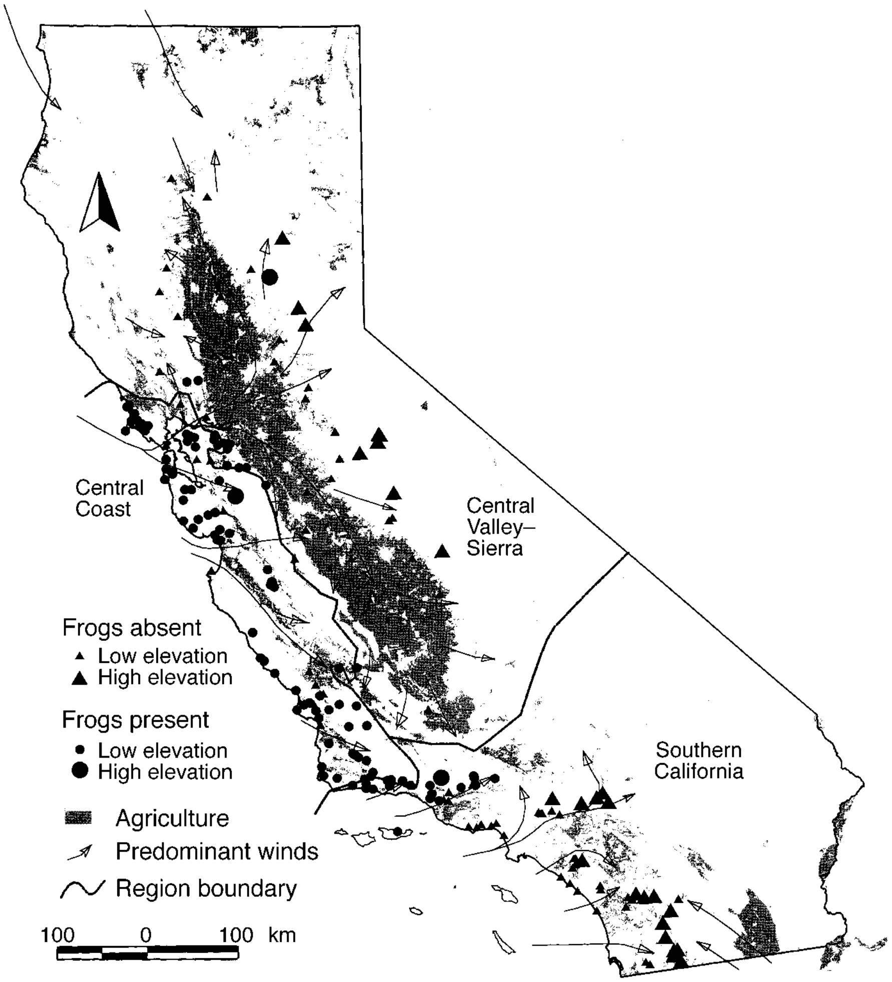

FIG. 2. Spatial patterns of decline of the California red-legged frog (*Rana aurora draytonii*). The map shows the location, current population status, and elevation of all historic frog sites (sites with at least one pre-1975 observation) used in our analysis. We also plot the distribution of agricultural lands based on U.S. Geological Survey land-use/land-cover maps, key predominant wind directions, and the boundaries of the three regions used in the regional analyses.

TABLE 1. Characteristics of present vs. absent sites for historic California red-legged frog sites.

| Variable | Frogs present† (mean ± 1 SE) | Frogs absent‡ (mean ± 1 SE) | *P*§ |
|---|---|---|---|
| Latitude (°) | 36.31 ± 0.1 | 35.54 ± 0.2 | <0.001 |
| Precipitation (cm) | 59.5 ± 2.2 | 59.6 ± 2.8 | 0.553 |
| Elevation (m) | 245 ± 20 | 514 ± 40 | <0.001 |
| Distance to AG (km) | 3.8 ± 0.5 | 3.6 ± 0.4 | 0.349 |
| Upwind distance AG | 22.9 ± 3.4 | 24.1 ± 3.8 | 0.762 |
| Percentage upwind AG | 2.9 ± 0.7 | 18.9 ± 2.5 | <0.001 |
| Percentage urban 2-km circle | 6.3 ± 1.2 | 11.2 ± 1.6 | 0.003 |
| Percentage AG 2-km circle | 6.6 ± 1.3 | 10.7 ± 1.8 | 0.023 |
| Percentage AG 200-km square | 16.3 ± 0.7 | 14.9 ± 0.9 | 0.001 |
| Percentage AG random triangle | 16.3 ± 1.8 | 12.2 ± 1.6 | 0.486 |

*Note:* AG = agricultural land use.

† $n = 124$.

‡ $n = 113$.

§ Mann-Whitney rank test of difference of means.

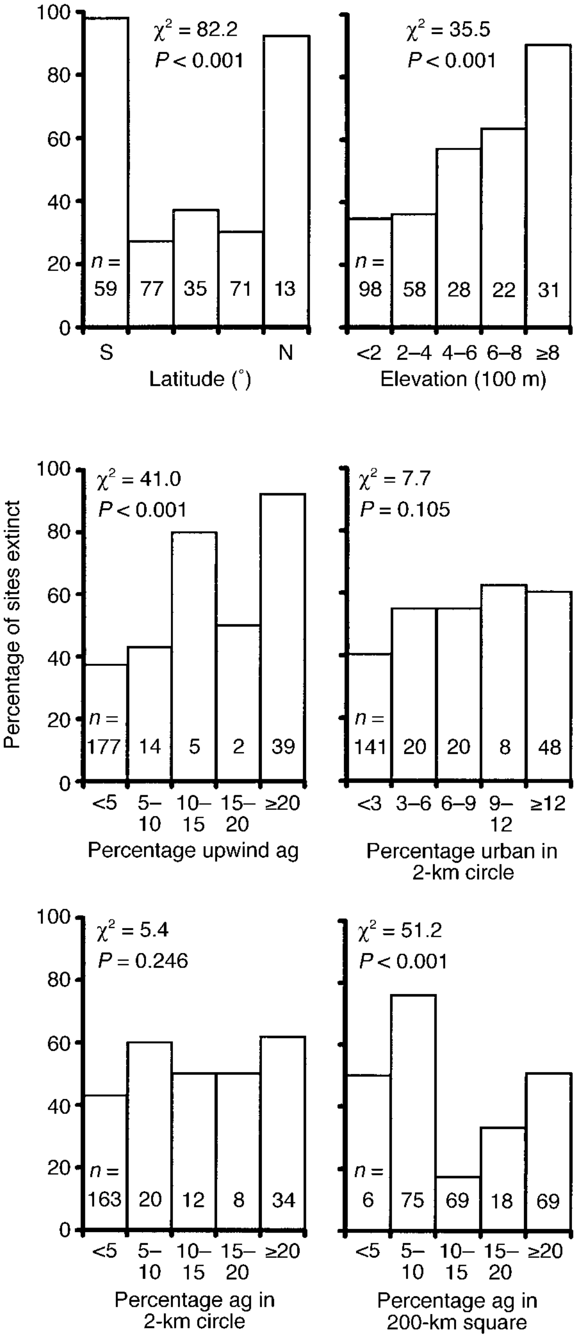

FIG. 3. Categorical variable graphs and associated $\chi^2$ tests of the relationship between populations status and latitude, elevation, percentage upwind agricultural land use (ag), percentage urban land use in a surrounding 2-km radius circle, and percentage agricultural land use in 2- and 200-km radius circles for the statewide analysis of California red-legged frog sites. Inset numbers indicate *n* values.

tionship between population status and categorical variables for elevation and percentage upwind agricultural land use, as well as gradients in declines for both of these factors (Fig. 3). The results of the categorical analysis for upwind agriculture should be interpreted with some caution, because the low number of sites in the middle categories (a total of 21 sites in the 5–20% categories) makes it difficult to distinguish between a gradient and a threshold response. The relationship between population status and latitude as a categorical variable was also significant. However declines did not show a north-to-south gradient as predicted by the climate change hypothesis, but greater declines in both the north and south (Fig. 3). The relationship between population status and percentage surrounding urban land use as a categorical variable was not significant ($P = 0.10$), although there was a shallow, but fairly consistent increase in declines with increasing urbanization. As categorical variables, neither percentage agriculture within a 2-km radius nor in a 200-km square showed a clear relationship with population status (Fig. 3).

None of the correlation coefficients between variables were $>0.5$, with the exception of the 0.63 correlation between latitude and agricultural land use in the 200-km square, suggesting that the variables in our analyses are not highly colinear. The correlation between elevation and upwind agricultural land use was 0.21, confirming that these two critical variables are statistically independent for our sites.

### *Multivariate analysis of patterns of decline*

The results of the statewide multivariate analysis were similar to the univariate analyses, except that the surrounding agricultural land use variables were not significant. Only latitude, elevation, percentage upwind agricultural land use, and percentage urban surrounding land use remained in the reduced model (Table 2). The likelihood ratio test for including all other variables as a group was not significant ($G = 10.15$, df $= 5$, $P = 0.07$). The likelihood ratio test for the overall (statewide) model was significant, the Hosmer-Lemeshow goodness of fit test (Hosmer and Lemeshow 1989) indicated the data fit the model, and the model correctly classified population status at 82.7% of the sites (Table 2).

In logistic regression, the odds ratio (exp[*B*]; Table 2) indicates the change in the odds of the dependent variable (here, presence/absence of frogs at a site) for a one unit increase in the independent variable, all other independent variables held constant. Thus, for elevation in our statewide model, for every 10 m increase in elevation (the unit used in the model), the odds of a site having a "present" population decline by a factor of 0.9789. Similarly, for a single percentage point increase in the amount of upwind agriculture, the odds of a site having a present population decline by a factor of 0.9141. Put another way, all else held constant, a site with one percent more upwind agriculture than another is ~0.91 times as likely to have a present population as a site without the additional agriculture. Thus, the odds ratio provides a quantitative indication

TABLE 2. Logistic regression models.

| Variable | $B$ | 1 SE | $P$ | exp($B$) |
|---|---|---|---|---|
| Statewide reduced model† | | | | |
| Latitude | 0.0599 | 0.0127 | <0.0001 | 1.0618 |
| Elevation | −0.0213 | 0.0068 | 0.0017 | 0.9789 |
| Percentage upwind AG | −0.0898 | 0.0169 | <0.0001 | 0.9141 |
| Percentage urban 2-km circle | −0.0549 | 0.0123 | <0.0001 | 0.9465 |
| Statewide reduced model with regions‡ | | | | |
| Region | | | <0.0001 | |
| Central Coast vs. Central Valley–Sierra | −2.4491 | 0.6798 | 0.0003 | 0.0862 |
| Central Coast vs. Southern California | −3.5301 | 0.5379 | <0.0001 | 0.0293 |
| Elevation | −0.0200 | 0.0077 | 0.0096 | 0.9802 |
| Percentage upwind AG | −0.0553 | 0.0159 | 0.0005 | 0.9462 |
| Percentage urban 2-km circle | −0.0677 | 0.0145 | <0.0001 | 0.9346 |
| Central Valley-Sierra Nevada model§ | | | | |
| Percentage upwind AG | −0.0778 | 0.0215 | 0.0003 | 0.9251 |
| Southern California model‖ | | | | |
| Latitude | 5.5731 | 2.3417 | 0.0173 | 263.24 |
| Elevation | −0.2144 | 0.0915 | 0.0191 | 0.8071 |
| Distance to AG | 2.8549 | 0.5125 | 0.0173 | 2.8549 |
| Central Coast model¶ | | | | |
| Percentage AG 2-km circle | −0.0324 | 0.0176 | 0.0658 | 0.9681 |
| Percentage urban 2-km circle | −0.0500 | 0.0152 | 0.0010 | 0.9512 |

*Notes:* The dependent variable for all models is frogs present (=1) or absent. $G$ is the likelihood ratio test for overall model significance. $C$ is the Hosmer-Lemeshow goodness-of-fit test. Acc is the percentage of sites correctly classified as having present or absent populations. $B$ is the regression coefficient; exp($B$) is the odds ratio. Latitude is in tenths of degrees, and elevation is in tens of meters. AG = agricultural land use.

† For this model, $n = 237$; $G = 117$, df = 4, $P < 0.0001$; $C = 6.37$, df = 8, $P = 0.60$; Acc = 82.7.

‡ For this model, $n = 237$; $G = 157$, df = 5, $P < 0.0001$; $C = 8.4$, df = 8, $P = 0.4$; Acc = 83.1.

§ For this model, $n = 53$; $G = 26.0$, df = 1, $P < 0.0001$; $C = 5.8$, df = 8, $P = 0.67$; Acc = 83.0.

‖ For this model, $n = 84$; $G = 79.8$, df = 3, $P < 0.0001$; $C = 0.16$, df = 8, $P = 1.0$; Acc = 97.62.

¶ For this model, $n = 100$; $G = 13.7$, df = 2, $P = 0.001$; $C = 6.03$, df = 6, $P = 0.42$; Acc = 90.0.

of the magnitude of the effect of each independent variable.

To examine the potential for different patterns in different geographic regions, we reran the model with regions as a fifth variable. With regions in the model, the coefficients for all variables remained significant, with the exception of latitude ($P = 0.17$), indicating that the statewide effect of latitude is better explained by regional differences in declines. Therefore, we constructed a second model with latitude removed and regions included (Table 2). There were large regional differences in declines, with the odds of frogs present 12- and 34 times more likely in the Central Coast than in the Central Valley–Sierra and Southern California regions, respectively. In the new model, the coefficient of percentage upwind agriculture was reduced by 39%, indicating that approximately one-third of the upwind agricultural effect could be accounted for by regional differences in declines. A test for inclusion of the three possible pair-wise interaction terms between the model's three key variables (elevation × upwind agriculture, elevation × urbanization, and upwind agriculture × urbanization) indicated no significant interactions.

Tests for inclusion of all of the interaction terms between regions and elevation, urbanization, and upwind agriculture were insignificant ($G = 8.9$, df = 6, $P = 0.18$), indicating that the main model effects do not vary significantly across regions. Nonetheless, the separate regional regression models indicated that different variables predominate within each region (Table 2). For the Central Valley–Sierra region, upwind agriculture was the only significant variable, in spite of the fact that declines in the region are concentrated at higher elevations (Table 3). In the Central Coast region, only surrounding urban and agricultural land use in a 2-km radius circle were significant, indicating that local habitat alteration accounted for the relatively few declines in the region. This is consistent with the statewide model in that almost all sites in the Central Coast are low elevation (mean, 220 m) and have little upwind agriculture (mean, 2.3%). Thus, upwind agriculture and elevation are not significant variables in the separate Central Coast model, since they are essentially invariant over the range of values that are associated with California red-legged frog declines. In the Southern California region, latitude, elevation, and distance to agriculture were all significant. The large coefficient for latitude in the model (Table 2) was due to the concentration of absent sites in the south and present sites in the north (Fig. 2). However, this is largely an artifact of restricting our study to California and excluding sites further south in Baja California where the frog is still

TABLE 3. Characteristics of present vs. absent sites for California red-legged frogs by region.

| Sites | *N* | Latitude | Elevation (m) | Percentage upwind ag | Percentage local urban | Percentage local ag |
|---|---|---|---|---|---|---|
| Central Valley–Sierra | | | | | | |
| All sites | 53 | 38.0 ± 0.2 | 413 ± 57 | 38.2 ± 3.8 | 6.5 ± 2.0 | 12.7 ± 3.3 |
| Present sites | 14 | 37.6 ± 0.3 | 239 ± 62 | 8.4 ± 4.0 | 1.0 ± 0.6 | 10.0 ± 6.0 |
| Absent sites | 39 | 38.2 ± 0.2 | 476 ± 72 | 48.9 ± 3.6 | 8.4 ± 2.6 | 13.7 ± 4.0 |
| Southern California | | | | | | |
| All sites | 84 | 33.9 ± 0.07 | 531 ± 43 | 2.9 ± 0.7 | 8.0 ± 1.6 | 6.8 ± 1.3 |
| Present sites | 21 | 34.5 ± 0.03 | 319 ± 54 | 1.7 ± 0.5 | 3.0 ± 0.8 | 3.5 ± 1.0 |
| Absent sites | 63 | 33.7 ± 0.07 | 601 ± 52 | 3.3 ± 0.9 | 9.7 ± 2.0 | 7.9 ± 1.6 |
| Central Coast | | | | | | |
| All sites | 100 | 36.5 ± 0.13 | 220 ± 20 | 2.3 ± 0.6 | 10.4 ± 1.8 | 7.8 ± 1.6 |
| Present sites | 89 | 36.5 ± 0.13 | 229 ± 22 | 2.3 ± 0.7 | 8.0 ± 1.7 | 6.8 ± 1.5 |
| Absent sites | 11 | 36.6 ± 0.36 | 150 ± 46 | 2.2 ± 1.2 | 29.4 ± 6.3 | 16.2 ± 6.1 |

*Note:* Percentage local is percentage in a 2-km radius circle surrounding a site; ag = agricultural land use.

fairly common. Percentage upwind agriculture was not a significant variable, and, in Southern California, the amount of upwind agriculture was generally low (mean, 2.8%, Table 3).

### *Robustness analyses*

Our map of California red-legged frog presence and absence (Fig. 2) was completely consistent with the three other comparison data sets, with all four showing a pattern of nearly complete declines in the Sierra Nevada, the Central Valley, and southern California, and relatively few declines in the Central Coast. Our results were also independent of the method of population status determination (expert opinion vs. direct observation). In the reduced statewide regression model, likelihood ratio tests for the inclusion of interaction terms between the four main coefficients (latitude, elevation, percentage upwind agriculture, percentage urban land use) and a categorical variable for expert opinion vs. direct observation were all nonsignificant. Similarly, when we ran the same four-variable model using the direct-observation and expert-opinion data sets separately, none of the differences in the coefficients were significant (all *t* test *P* values exceeded 0.05). Even when we deleted the expert-opinion data entirely, our results remain qualitatively similar to those for the full data set. Mean values for nine site characteristics for direct-observation sites ($n = 111$) and the full data set are very similar and, based on Mann–Whitney tests, none are significantly different (the sole exception is the distance to agriculture, where present sites are farther from agriculture in the direct-observation data set). The coefficients of the statewide regression model run on the direct-observation data are not identical with those from the full data set, but none of the differences in coefficient values are statistically significant (Table 4).

In general, our results are very robust to errors in site status (Table 5). For the 10%-error simulation, all coefficients remained significant in all 10 runs; and, even with the 20%-simulated-error runs, the majority of the coefficients remained significant (latitude was significant in 90% of runs, elevation in 50%, percentage upwind agriculture in 100%, and local urban in 60%). None of the potential outlier sites in the regression models strongly influenced our results. In all cases, when a single site was dropped, or population status was switched, the significance of the four variables in the regression model was unchanged, and regression coefficients changed very little. The greatest change to a regression coefficient was a 21% increase in the coefficient for upwind agriculture, if the present site in Northwest Kern County with high upwind agriculture was dropped or switched to absent. Most other changes were in the 5–10% range.

In the spatial autocorrelation analysis, the 5-km minimum intersite distance requirement produced five data sets with 56–59 sites dropped. When we ran the reduced

TABLE 4. Comparison of direct observation vs. pooled data set logistic regression models.

| Variable | Pooled data set | | | Direct observation only | | | Difference |
|---|---|---|---|---|---|---|---|
| | *B* | 1 SE | *P* | *B* | 1 SE | *P* | *t* test |
| Latitude | 0.0599 | 0.0127 | <0.0001 | 0.0650 | 0.0188 | 0.0006 | 0.82 |
| Elevation | −0.0213 | 0.0068 | 0.0017 | −0.0121 | 0.0087 | 0.1637 | 0.41 |
| Percentage upwind ag | −0.0898 | 0.0169 | <0.0001 | −0.0835 | 0.0210 | 0.0001 | 0.82 |
| Percentage urban 2-km | −0.0549 | 0.0123 | <0.0001 | −0.0416 | 0.0169 | 0.0141 | 0.52 |

*Notes:* The pooled data set is with both direct observation and expert opinion data; *P* is the significance of the regression coefficient; the *t* test entries are *P* values for a *t* test of the differences between the regression coefficient for direct observation vs. the pooled data set; ag = agricultural land use.

TABLE 5. Logistic regression with simulations of 10% and 20% site status errors.

| Simulation parameter | Latitude | Elevation | Percentage upwind ag | Percentage local urban |
|---|---|---|---|---|
| $B$, statewide model | 0.0599 | −0.0213 | −0.0898 | −0.0549 |
| Min. $B$, 10% errors | 0.0334 | −0.0104 | −0.0494 | −0.0229 |
| Max. $B$, 10% errors | 0.0481 | −0.0187 | −0.0630 | −0.0454 |
| No. runs $P < 0.05$ | 10 | 10 | 10 | 10 |
| Min. $B$, 20% errors | 0.0085 | −0.0052 | −0.0161 | −0.0070 |
| Max. $B$, 20% errors | 0.0306 | −0.0141 | −0.0430 | −0.0370 |
| No. runs $P < 0.05$ | 9 | 5 | 10 | 6 |

*Notes:* In each simulation, population status was switched at 10% or 20% of all sites chosen at random. The 10% and 20% simulations were each run 10 times, and the statewide logistic model was recalculated on each run. $B$ is the logistic regression coefficient. ''No. runs $P < 0.05$'' indicates the number of simulation runs for the 10% or 20% error simulation in which the coefficient for a variable was significant at the $\alpha = 0.05$ level.

four-variable logistic regression model on these data sets, all coefficients remained significant. The 10-km minimum intersite distance produced 5 data sets with 94–99 sites dropped. Again, all regression coefficients remained significant, with the exception that in one data set the $P$ value for the elevation coefficient was 0.0522.

Although we restricted our primary analyses exclusively to historic sites (those with a date of first observation before 1975), the reduced model was largely unchanged by the inclusion of 102 nonhistoric sites in the dataset (all coefficients significant and magnitudes changed <25%). Inclusion of the 26 completely urbanized sites strengthened the effect of surrounding urban land use (the two univariate tests became significant), however it did not otherwise change our results. Finally, regression results were independent of whether or not location records for a site included a verified museum specimen. Likelihood ratio tests for the inclusion of interaction terms between the four model variables and the categorical variable for site with verified museum specimen were all nonsignificant.

## DISCUSSION

The spatial analysis of patterns of decline is a powerful and rapid method for screening potential causal factors that have led to the widespread disappearance of the California red-legged frog. This strategy is not a replacement for experimental studies of specific mechanisms (e.g., Blaustein et al. 1994, Lawler et al. 1999), but rather a complement to such approaches. Compared to long-term, longitudinal studies of individual sites (Semlitsch et al. 1996, Trenham et al. 2000) large-scale spatial analyses may be better able to detect long-term patterns of change (Shaffer et al. 1998), although without the demographic detail provided by intensive longitudinal studies. In particular, the small sample sizes, high population variances, and corresponding low statistical power to detect changes that often plague longitudinal studies are not at issue with broad-scale spatial analyses. Thus, these two strategies can work together to provide a comprehensive view of population trends: intensive longitudinal studies provide a detailed view of one or a few sites, and broad spatial analyses can test those patterns at a landscape level.

In this study, we specifically address the predictions generated by four of the most widely cited causes of amphibian declines as they apply to California populations of *R. a. draytonii.* We discuss each in turn, as well as the disease and introduced-exotics hypotheses for this species.

### *Climate change*

The spatial pattern of declines of the California red-legged frog is not consistent with that predicted by the climate change hypothesis. As predicted by the hypothesis, the mean latitude for extirpated sites is significantly to the south of the mean for extant sites, and latitude has a significant positive coefficient in the reduced regression model without regions (Table 1). However, the univariate categorical analysis (Fig. 3), the multivariate model with regions (Table 2), and inspection of the pattern of declines indicate that there is not a clear latitudinal gradient in declines. This conclusion is reinforced by the observation that, at the southern limits of *R. a. draytonii* in the San Pedro Martir Mountains in Baja California, Mexico, the frog is still fairly common in some areas (L. Grismer, *personal communication*). The lack of a clear north–south gradient in declines, combined with the *increase* (rather than predicted decrease) in declines with elevation, and the lack of an association of declines with mean precipitation all argue against climate change as a cause of red-legged frog declines.

### *UV-B*

Declines of California red-legged frogs show a clear elevational gradient, with greater declines at higher elevations (Table 1, Fig. 3). To our knowledge, this is the first quantitative assessment, within a single species, of the widespread perception that amphibian declines are more pronounced at higher elevation (Wake 1991). Although populations at the very upper end of the species' elevational range might experience greater declines due to isolation, or possibly physiological stress, this would not produce the consistent elevation gradient that we observe. The elevational gradient in declines is consistent with the UV-B radiation hypothesis, and therefore UV-B may be a contributing factor to California red-legged frog declines. However, the UV-B hypothesis also predicts a north-to-south gradient in declines (with greater declines predicted as one moves south), and we find no such pattern (see *Discussion: Climate change*). How to weigh the conflicting results of an elevational gradient in declines with the lack of a latitudinal gradient in declines partly depends upon which pattern might predominate. The elevational range of *R. a. draytonii* is ~1 km, ranging from sea level to a maximum of 1700 m, but with most sites <1000 m in elevation (94% of the historic sites in this analysis). Based on theoretical models and empirical observations, UV-B is expected to increase by 5–6% for every 1-km increase in altitude for perfectly clear, cloudless skies with unpolluted air (S. Madronich, *personal communication*). However, tropospheric pollutants, aerosols, and fog may greatly reduce UV-B exposure at low elevations, producing elevational gradients that have been measured outside California ranging from 30% to 60% per kilometer (Blumthaler 1993, Cabrera et al. 1995). To assess latitudinal changes in UV-B along a north–south transect through our study area, we used data for 1979–1992 on monthly estimated erythema UV-B dose from the Nimbus 7/TOMS satellite (S. Madronich, B. Mayer and C. Fisher, *unpublished manuscript*). Our transect consisted of nine contiguous satellite ''views'' (single UV-B estimates made in a 1° latitude × 1.25° longitude window) running from Redding in the north to Mexicali in the south. Annual mean erythema UV-B exposure at the southern end of this transect is 28% higher than at the northern end, with an even gradient in between. However, the north-to-south difference in UV-B exposure changes dramatically by season, rising to 135% in December and falling to just 2% in July. Given the unknown magnitude of actual elevational differences in UV-B, and the huge seasonal differences in the latitudinal differences, it is unclear whether the predicted latitudinal or elevational gradients of declines should predominate.

The sensitivity of California red-legged frogs to UV-B is unknown. No effect of near-sea level, ambient UV-B has been found on hatching success (Blaustein et al. 1996, Ovaska et al. 1997) or larval survival (Ovaska et al. 1997) for the related northern red-legged frog (*R. a. aurora*), although enhanced UV-B (above ambient at sea level) had significant negative effects on *R. a. aurora* hatching success and larval survival (Ovaska et al. 1997). These results suggest that increased UV-B levels may be important for northern red-legged frogs, although results for *R. a. aurora* should not automatically be assumed to apply to *R. a. draytonii*. Biochemical, morphological, and behavioral studies (Hayes and Miyamoto 1984, Green 1985, Hayes and Kremples 1986) and mitochondrial DNA analysis in progress (H. B. Shaffer, *unpublished data*) all suggest the two taxa should be treated as distinct entities, and as such may differ in their response to UV-B. For example, Anzalone et al. (1998) found that ambient levels of UV-B negatively affected hatching success of *Hyla cadaverina*, but not its sister taxon *H. regilla*. Given the mixed results of our analysis (a strong elevational gradient, but no latitudinal gradient), the absence of UV-B research on *R. a. draytonii*, and the possibility of sublethal effects and synergisms with other factors such as disease (Kiesecker and Blaustein 1995) and contaminants (Long et al. 1995, Hatch and Burton 1998), we consider UV-B to be a potential factor that awaits further study.

### *Wind-borne agrochemicals*

Our observed association of declines with the amount of upwind agricultural land use suggests that wind-borne agrochemicals may be an important factor in declines of the California red-legged frog. For all sites, the percentage of upwind land in agriculture for sites where *R. a. draytonii* has disappeared is 6.5 times greater than for sites where they persist (18.9% vs. 2.9%; Table 1), and there is a strong relationship between increasing levels of upwind agriculture and the percentage of extirpated sites (Fig. 3). The pesticides hypothesis predicts that declines would be associated with both the amount of upwind agriculture and the distance to the nearest agricultural land use. While declines were strongly associated with the amount of upwind agricultural land use, they were not associated with upwind distance to agriculture. This may be because our proximity metric only considers the nearest patch and, therefore, is sensitive to the position of even the smallest patches of agricultural land use. To assess the joint effect of upwind agricultural area and proximity, we constructed an upwind agricultural index by dividing all agricultural land within the upwind triangle into patches with maximum extent of 10 km$^2$, and then summing across all agricultural patches the area of the patch divided by the distance of the patch centroid to the frog site at the upwind triangle's vertex. This index thus combines both area and distance of agricultural lands into a single measure. The mean value of the index was 4.2 times greater at absent sites than at present sites (mean present, 3615; mean absent, 15 232; $P < 0.001$, Mann-Whitney test) and the index performed similarly to the percentage upwind agricultural land use variable in the statewide logistic regression model. The association of declines with upwind agriculture holds for California as a whole, is not significantly different between the regions (based on the interaction tests), and is particularly pronounced within the Sierra Nevada–Central Valley region where agricultural activity is greatest (Table 2).

This strong association of declines with the amount of upwind agricultural land use is not just a reflection of habitat alteration due to agriculture. We can test this in three ways. First, whereas the amount of upwind agricultural land use is associated with declines, the amount of agricultural land use in a random direction is not (Table 1). Second, when we analyzed the amount of agriculture in a 200-km square centered on each site, there was actually slightly greater agricultural land use surrounding sites with present populations than sites with absent populations. This pattern is exactly the opposite of what one would expect if the upwind agricultural land use measurements were simply reflecting surrounding agricultural land use. And third, neither the amount of surrounding agricultural land use in a 2-km circle nor in a 200-km square were associated with declines in either the categorical variable analyses, nor in the multivariate analysis.

In general, relatively little is known about the fate of pesticides (transport, dissolution, degradation, and deposition onto soil, plants, and water) and their impact on ecosystems in the topographically complex landscape of California. However, a number of studies for the Sierra Nevada have documented the transport and deposition of pesticides originating in the Central Valley. Zabik and Seiber (1993) found organophosphate pesticide residues (chlorpyrifos, diazanon, and parathion) in wintertime air and precipitation samples from sites at 533-m and 1920-m elevations in Sequoia National Park in the southern Sierra Nevada. They found that quantities of pesticides decreased with increased distance and elevation from agricultural lands in the Central Valley floor. In the same locations, Aston and Seiber (1997) found summertime transport and deposition of pesticide residues on pine tree needles. At other sites, McConnell et al. (1998) found organophosphate pesticides in winter and spring rain and snow both in the southern Sierra and further north in the Lake Tahoe region. In some cases, pesticide levels were, in their words, ‘‘uncomfortably close’’ to the published median lethal concentrations (LC50) for *Gammarus fasciatus,* an amphipod used by the U.S. Environmental Protection Agency for water quality assessment. Pesticides have been found in the bodies of frogs and fish in the Sierra Nevada, beginning with Cory et al.’s (1970) finding of DDT residues in the bodies of mountain yellow-legged frogs (*Rana muscosa*) throughout the Sierra. More recently, Datta et al. (1998) found PCBs and organophosphate pesticides in the bodies of trout and Pacific treefrog (*Hyla regilla*) tadpoles from the southern Sierra Nevada.

A potentially confounding aspect of the upwind agriculture pattern is the co-occurrence of low upwind agriculture levels with near-coast habitats. Although we know of no hypothesis for amphibian decline that would predict survival in areas downwind from the ocean and declines inland, it is clear from Fig. 2 that red-legged frogs mainly persist near the coast (although this is not the case in southern California). The amount of upwind agricultural land use is negatively correlated with the percentage of upwind area that is over ocean (Pearson correlation, $-0.85$), thus it is possible that our interpretation of a negative influence of upwind agriculture is, in reality, an unknown positive influence of upwind oceanic air. Alternatively, the inverse correlation may reflect the identical phenomenon: air downwind from agriculture may carry pollutants, while air coming off the ocean is relatively clean. Our work in progress on a number of other declining California amphibians indicates a similar association of declines with upwind agricultural land for inland species where upwind oceanic air is not a factor, leading us to conclude that upwind pesticides or other agrochemicals are the most likely interpretation for this pattern.

### *Habitat destruction*

It is clear that habitat alteration and destruction due to urbanization have contributed to declines of the California red-legged frog. Even though we restricted our main analysis to sites that are not completely urbanized and where at least some suitable frog habitat still exists, we still find an association of declines with percentage surrounding urban land use. If we include sites that have been completely urbanized in the analysis, then the impact of urbanization is even stronger. Results for surrounding agricultural land are mixed, but they do not indicate a strong association between surrounding agricultural land use and declines. This may be because, unlike urban land use, the total extent of agricultural land use has been declining over the last 25 yr (California Economic Development Agency 1974, 1998), making it unlikely that the relatively recent declines analyzed here would be associated with habitat destruction due to agriculture. If so, then in areas such as Santa Barbara and San Luis Obispo Counties, where vineyards are expanding rapidly, we may see negative impacts on red-legged frogs in the future.

### *Other potential factors*

We were not able to analyze the spatial implications of two other important hypotheses for declines: disease (Bradford 1991, Carey 1993, Berger et al. 1998, Lips 1998, Lips 1999) and introduced species (Moyle 1973, Hayes and Jennings 1988, Fisher and Shaffer 1996, Knapp 1996, Lawler et al. 1999, Knapp and Matthews 2000). Not enough is known about the biology of possible disease agents, such as the chytrid fungus (Berger et al. 1998), to generate spatial implications that could be tested. For exotic species, there is much more biological information available. Moyle (1973) surveyed 130 stream sites in the southern Central Valley, and found bullfrogs but no California red-legged frogs, and attributed the absence of red-legged frogs to bullfrog predation and competition. Hayes and Jennings (1988) also found a negative association between the presence of red-legged frogs and bullfrogs in the Central Valley, and Fisher and Shaffer (1996) found a negative association between the presence of introduced predators and several other native amphibian species in the Central Valley. In field experiments, Lawler et al. (1999)

found that postmetamorphic bullfrogs preyed on California red-legged frog tadpoles, significantly reducing mean tadpole survival. Mosquitofish, (another introduced predator) were also found to reduce the mass of new metamorphs (Lawler et al. 1999), and this reduced size at emergence has cascading fitness consequences on adult survival in other amphibian species (Smith 1987, Semlitsch et al. 1988).

Ideally, one could test the exotic-predator hypothesis by comparing the pattern of declines with the distribution of specific exotic species, such as bullfrogs, mosquitofish, or other predatory fishes. In this case, however, there are several difficulties with such an approach. Because we do not have data on the status of exotic species at each site, we cannot perform a site-by-site analysis of the association of red-legged frogs and exotics. On a broader scale, bullfrogs and mosquitofish are distributed widely in the state, and they occur both in areas where red-legged frogs have persisted and where they have declined. Therefore, a broad-scale analysis based upon presence and absence of these predators could not explain the regional patterns of frog declines seen in Fig. 2. Furthermore, in the western United States, the introduction of exotic aquatic species has been facilitated by habitat alterations, making it difficult to disentangle the effect of exotics from that of habitat alteration (Hayes and Jennings 1988). For example, within the Central Valley, Fisher and Shaffer (1996) found an up-slope shift in the distribution of several native amphibians that they attributed to introduced predators, habitat modifications at low elevations, or both. Consistent with this observation, we found that, within the Central Valley proper, sites with red-legged frogs present were on average at higher elevations (mean, 177 m; $n = 11$) than sites with frogs absent (mean, 91 m; $n = 12$), which is the opposite of the statewide pattern. However, we also found within the Central Valley that low-elevation sites ($<150$ m) on average had 33.1% combined agricultural or urban land use in a 2-km radius circle surrounding the site, whereas sites $>150$ m had 19.8% agricultural-plus-urban surrounding land use, suggesting that low-elevation sites are generally more disturbed than higher elevation Central Valley localities. In addition, site-specific studies suggest that bullfrogs and red-legged frogs can apparently coexist in some places (Cook 1998; S. Christopher, *personal communication*), indicating that introduced predators do not always exclude red-legged frogs from a site.

In summary, pathogens and introduced exotics undoubtedly both play a role in the decline of many amphibians, including California red-legged frogs, and their importance probably varies on a site-by-site basis depending on overall habitat quality, refugia, and synergisms with other factors. Understanding the impact of exotic predators on red-legged frogs may require information on predator abundance coupled with habitat characteristics influencing potential refugia. Unfortunately, this type of information was not available for multiple sites across the range of *R. a. draytonii* to allow us to analyze the spatial patterns of decline and test the exotic-predator hypothesis.

## CONCLUSIONS

What should we make of the spatial patterns presented here, and the spatial analysis of causal factors in general? First and foremost, multiple processes can generate similar patterns; therefore, the link between observed patterns and presumed underlying processes must be made with caution. Conversely, given potential confounding factors, the absence of pattern should not be taken as proof of the absence of a process. Even with these qualifications, there are at least two important roles for the spatial analysis presented here. First, while field and laboratory experiments on individual organisms are vital to understanding possible mechanisms causing declines, such experiments are necessarily restricted to individuals or small local populations. Population changes above the local-site level cannot be subjected to experiments, and can only be quantified and analyzed through large-scale observational studies. Spatial analysis is a valuable approach for examining large-scale observational data and associating declines with plausible mechanisms.

Second, the spatial results we have presented generate clear predictions that can be tested with field and laboratory studies. For example, field studies could test the relationship between pesticide levels at a site, the amount of upwind agricultural land use, and frog declines. We hope that our work will encourage further investigation of the role of agrochemicals in amphibian declines, given that to date there has been relatively little research on this hypothesis for declines. The Sierra Nevada has been the subject of some recent toxicological work (Zabik and Seiber 1993, Aston and Seiber 1997, Datta, 1997, Datta et al. 1998, McConnell et al. 1998), but similar studies have not been conducted in other areas of California or elsewhere where declines have occurred. For example, in both Central America and Australia, major amphibian declines (Ingram and MacDonald 1993, Richards et al. 1993, Pounds and Crump 1994, Lips 1998, 1999) have occurred in areas close to, and downwind for part of the year from, large agricultural zones. To date, very little contaminants research has been conducted in these areas. Even when pesticide residues are found in frogs (Cory et al. 1970, Datta et al. 1998), we do not understand the biological relevance of these residue levels. This is particularly true for sublethal effects, such as interference with hibernation or immune system suppression (Carey and Bryant 1995, Stebbins and Cohen 1995, Taylor et al. 1999).

Our analysis indicates that multiple factors may be responsible for declines of the California red-legged frog. At a number of sites, declines are associated with urbanization. We find a strong elevational gradient in declines, which may be due to UV-B, although our test of the UV-B hypothesis produced mixed results. Finally, declines are associated with the amount of upwind agricultural land use, suggesting that wind-borne agrochemicals may be contributing to declines.

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## APPENDIX

Site locations and sources are available online in ESA's Electronic Data Archive: *Ecological Archives* A011-009.