
The Decline of Amphibians in California's Great Central Valley

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Abstract: *Declines in amphibian populations are rarely reported on the community or ecosystem level. We combined broad-scale field sampling with historical analyses of museum records to quantify amphibian declines in California's Great Central Valley. Overall, amphibians showed an unambiguous pattern of decline, although the intensity of decline varied both geographically and taxonomically. The greatest geographical decline was detected in the counties of the Sacramento and San Joaquin Valleys. Two species, *Rana aurora* and *Bufo boreas* were identified as the most affected by decline, whereas *Pseudacris regilla* was the least affected. The Coast Range counties had little or no detectable decline. We provide new evidence implicating introduced predators as a primary threat. Introduced predators occur at lower elevations than native species, and our data indicate that for some native species there has been significant restriction to higher elevation sites from a formerly broader distribution. Our historical approach provides a strategy for identifying declining amphibian communities that complements more detailed, long-term monitoring programs and provides an assessment of the pattern of change that is a necessary prerequisite for the development of field experiments that test hypothesized mechanisms of change.*

La declinación de anfibios en el Gran Valle Central de California

Resumen: *Las declinaciones de anfibios raramente son reportadas a nivel comunidad o ecosistema. Combinamos muestreos de campo a gran escala con análisis históricos de registros en museos para cuantificar las declinaciones de anfibios en el Gran Valle Central de California. En general, los anfibios mostraron un patrón de declinación muy claro, aunque la intensidad de declinación varió tanto geográfica como taxonómicamente. La mayor declinación geográfica se detectó en los condados y los valles de Sacramento y San Joaquín. Dos especies, *Rana aurora* y *Bufo boreas*, fueron las más afectadas por la declinación, mientras que *Pseudoacris regilla* fue la menos afectada. La declinación en los condados de franja costera fue pequeña o no detectable. Proporcionamos evidencia de que depredadores introducidos son la principal amenaza. Los depredadores introducidos ocurren en elevaciones menores que las especies nativas, y nuestros datos indican que algunas especies nativas han sido significativamente restringidas a sitios de mayor elevación a partir de una distribución original más amplia. Nuestro enfoque histórico proporciona una estrategia para identificar la declinación de comunidades de anfibios que complementa a los programas de monitoreo detallado y a largo plazo y proporciona una evaluación del patrón de cambio que es un prerequisite para el desarrollo de experimentos de campo para probar mecanismos hipotéticos de cambio.*

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Paper submitted July 13, 1995; revised manuscript accepted December 1, 1995.

Introduction

Regional and global amphibian declines have attracted a great deal of attention and controversy (Blaustein & Wake 1990; Blaustein 1994; Blaustein et al. 1994c; McCoy 1994; Pechmann & Wilbur 1994; Travis 1994). The controversy has centered on the resolution of two questions. First, to what extent are "declines" a real phenomenon rather than a misinterpretation of the large fluctuations in population size that characterize many natural amphibian populations (Heyer 1979; Corn & Fogelman 1984; Pechmann et al. 1991; Dodd 1992; Hairston & Wiley 1993; Kagarise Sherman & Morton 1993)? Second, if declines are real, are they caused by global environmental change or by localized anthropogenic factors (Barinaga 1990; Blaustein & Wake 1990; Blaustein et al. 1994c)? Although documenting the existence of declines should logically precede the search for causal mechanisms, the urgency of understanding, and reversing, the wholesale collapse of worldwide amphibian populations has motivated a search for causes even as amphibian biologists debate the reality of global patterns of decline (Barinaga 1990; Blaustein & Wake 1990; Blaustein 1994; Blaustein et al. 1994a,b; McCoy 1994; Pechmann & Wilbur 1994; Travis 1994).

Part of the frustration in documenting declines in any species or community is the historical nature of the problem (Reznick et al. 1994). We must understand the past distribution and abundance of species to make meaningful comparisons with the present. The key problem, then, is how to quickly and accurately compile both historical and current information for entire amphibian communities, while maintaining high statistical and field methodological standards. This task appears daunting, especially at large geographic scales, but we feel that a focused program of field surveys and historical analyses of museum records can provide insights into both the patterns and mechanisms of amphibian decline prior to choosing sites for long-term monitoring programs or field experiments. Although such data will almost necessarily be less complete than one might desire, they often provide the only form of historical information available for many amphibian communities that are currently under scrutiny. As Reznick et al. (1994) point out, museum collections may be used to quantify the local abundances of individual species (if census data for specific sites are available) or to investigate shifts in species composition of entire drainages or other large regions. Although direct comparisons of specific sites are obviously important, this approach requires that current sampling be conducted at precisely the same sites, and with the same methods, as they were in the past (Barry & Shaffer 1994; Drost & Fellers 1994). Unfortunately, few past studies were complete and rigorous enough to facilitate such direct comparisons, making this strategy of limited general utility.

In the absence of well-controlled field sampling programs in the past, how can one collect meaningful data

on the historical decline of amphibian communities? We submit that even with the relatively incomplete samples that typify most museum collections, one can still use this information to glean important insights into historical patterns of distribution, and thus current patterns of decline. We provide an example utilizing the entire community of pond breeding amphibians in California's valley oak-grassland and prairie habitats throughout the Great Central Valley and Coast Range (Fig. 1). This grassland-dominated landscape has long been recognized as a discrete ecological and biogeographical community (Hickman 1993). We follow Hickman (1993) in recognizing three subcommunities that represent different drainage systems in Fig. 1: the Coast Range, the Sacramento Valley, and the San Joaquin Valley. Six amphibian species were historically widespread in this habitat and a single aquatic breeding site would generally contain between two and five species (Feaver 1971; Barry & Shaffer 1994; Fisher, unpublished).

Methods

Between 1990 and 1992 we surveyed aquatic habitats for reproductive populations of pond-breeding amphibians

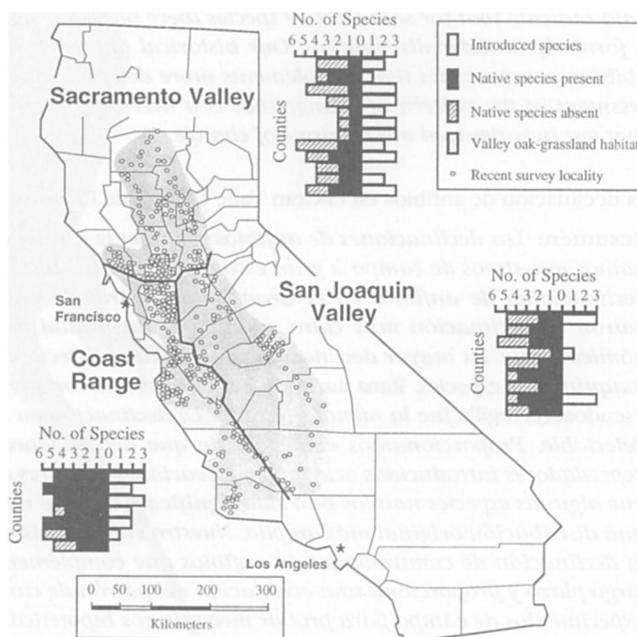


Figure 1. Aquatic sites surveyed for native amphibians in California during 1990–1992. Vertical Histograms indicate the numbers of native and introduced species present (from current field surveys) and native species absent (by subtraction, from historic museum data) by county within each subregion. The counties of each subregion are plotted on the histogram from top to bottom. The first county is the one furthest west and north, and the last one is the furthest east and south, they progress in order from west to east.

ans. We considered a population reproductive if it contained larvae during the appropriate months of the winter or spring. We sampled vernal pools, natural and artificial ponds, and marshlands for larval amphibians during the late winter and spring to maximize our ability to detect this breeding activity (Barry & Shaffer 1994; Heyer et al. 1994). A few sites were sampled several times across years and seasons to determine the period of greatest larval abundance for the regional sampling of localities. Under natural conditions vernal pools are ephemeral and fill relatively synchronously. Therefore, most larvae tend to use ponds during the same period of time, and sites could be sampled once during a season to determine the presence of a species at a site. We sampled ponds with 3- to 6-mm mesh seine nets (Shaffer et al. 1994; Fisher 1995). From 1986 to 1994 we sampled over 1000 aquatic sites, although for this analysis we only included the 315 ponds (from 28 counties) for which we had a complete survey of biotic data. These sites cover most of the extant distribution of the valley oak-grassland/prairie community except for a small section of the Monterey Bay coast where the extremely fragile populations of Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*) occur (Russell & Anderson 1956).

Our sampling protocol was designed to sample localities evenly across wide areas to detect regional patterns of current species distribution. We generally maintained a distance of 10-30 km between sites unless suitable habitat was not available (in which case the distances between sites were greater). If an abundance of excellent habitat was available we sampled more intensively. To maximize the chances of locating breeding activity if it was present, we concentrated on aquatic sites that, in our subjective view, were "good" amphibian breeding habitat. In vernal pool complexes with variable pond sizes, we concentrated our sampling in the largest pools because they generally harbor the greatest amphibian diversity. By concentrating on the (apparently) best amphibian habitat, our localities represent the minimum number of reproducing populations of amphibians. Thus, they should not be considered a definitive reference for the presence or absence of amphibians in an area but rather a reasonable indication of the patterns of amphibian breeding activities in prime habitat in a given region. We used counties as our geographical unit for analysis because our inability to find even a single locality for a species in a county seems a reliable indication that it is either rare or absent in a region.

We recorded the presence or absence of the following native amphibians for each pond: California newt (*Taricha* spp. including both *T. granulosa* and *T. torosa torosa*, but not the stream and river inhabitant, *T. torosa sierrae* from the Sierra Nevada foothills); California tiger salamander (*Ambystoma californiense*); Pacific treefrog (*Pseudacris (Hyla) regilla*); western spadefoot toad (*Scaphiopus hammondi*); western Toad (*Bufo boreas*);

and California red-legged frog (*Rana aurora*). We also surveyed for introduced species (frogs and fish): *Gambusia affinis* (mosquito fish), fish (all other species of fish found in any ponds, all of which were usually introduced), and *Rana catesbeiana* (bullfrog). Mosquito fish were recorded separately from other fish because they are intentionally introduced as biological control agents and are known predators of amphibian eggs and hatchlings (L. Kats, personal communication; P. Trenham, personal communication; Grubb 1972). We did not sample intensively for each individual species of introduced fish because several species may be present in a single pond, and they appear to have similar ecological effects on native amphibians. Rather, after it was established that native amphibians were or were not present, we moved on to the next pond. Questionable identifica-

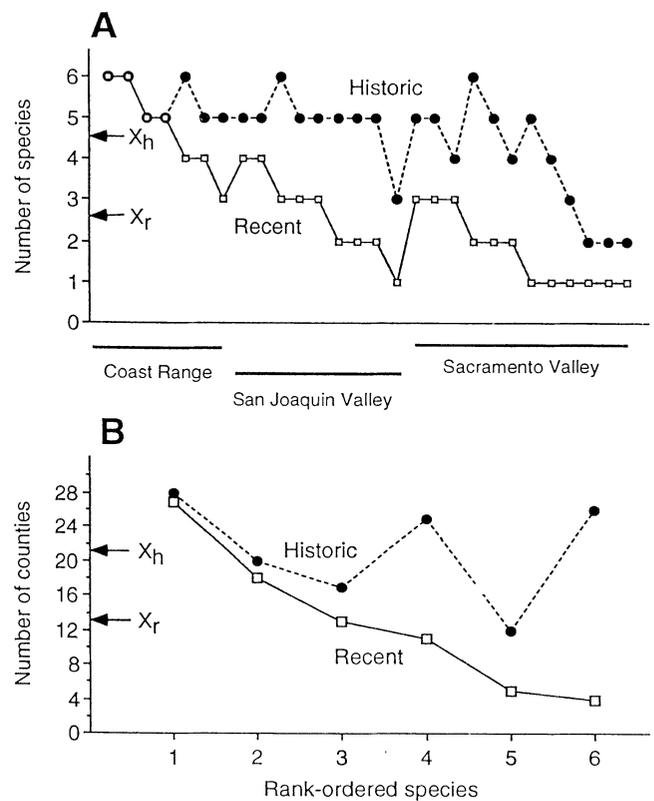


Figure 2. The number of native amphibian species found in each of 28 counties in three subregions of the Great Central Valley historically and during our surveys. Counties are rank ordered within each region by the number of recent species occurrences. The mean number of species per county historically (X_h) differs from that in our surveys (X_r ; paired *t* test, $p < 0.0001$) (A) and the number of counties in which each species occurs, historically and during our surveys (B: 1, *P. regilla*; 2, *A. californiense*; 3, *S. hammondi*; 4, *B. boreas*; 5, *Taricha* spp.; 6, *R. aurora*); X_h and X_r are the mean numbers of counties per species historically and from our surveys, respectively.

tions were confirmed by P. Moyle (fishes) and M. Jennings (amphibians). Elevation and several other biotic and abiotic parameters were measured at each site for a separate, ecological study of amphibian population ecology (Fisher 1995).

Historic distribution data were compiled for the six native species based primarily on museum specimens from the California Academy of Sciences and the Museum of Vertebrate Zoology (University of California, Berkeley) because these two collections house the greatest numbers of specimens from the study region and incorporate the most individual localities. These data were supplemented with unpublished data (Mark Jennings) for *R. aurora*, *P. regilla*, and *S. hammondi*. *Ambystoma californiense* records were extracted from California Department of Fish and Game's Natural Diversity Data Base, whereas those for *R. catesbeiana* were taken from Bury and Luckenbach (1976). Historic occurrences were only included in our determination of the past distribution of a species if they were collected from our sampling region. We recorded historical elevations from the California Department of Fish and Game's data base for all available localities of *A. californiense* and determined elevations for *S. hammondi* and *B. boreas* using topographic maps. We examined these three species in detail because the number of current and historic records for them were very similar, suggesting that a direct comparison of average elevations over time would be meaningful.

Almost all of the historic records in this database are from the 1890s-1980, and we consider them to represent a reasonable sample of the recent historic range for these species. However, a few counties appear to be systematically under-sampled. We deleted Kings County

from the analysis because only two individual amphibian specimens are known from the county. We retained Sutter, Yuba, and Placer counties in our analysis, even though several species that probably "should" have been historically present could not be confirmed in museum collections. If the historical records for these counties are an inadequate representation of the true distribution of several common species, this will render our estimates of decline conservative because these counties would actually contain a greater loss of species than we detected due to inadequate historical sampling.

Results

Distributional Trends across the Great Central Valley

We documented a statistically significant decline in the number of species currently found in most counties compared with that found historically, supporting the interpretation that a community-wide decline has occurred (Fig. 2A). This decline varies both geographically (Fig. 2A) and taxonomically (Fig. 2B). Geographically, the Coast Range habitat shows relatively little overall decline (mean difference in number of species/county between current and historical records = 0.71), whereas the Sacramento and San Joaquin Valleys both show larger, virtually identical declines (San Joaquin Valley, mean difference = 2.22; Sacramento Valley, mean difference = 2.08; Kruskal-Wallis Test comparing the three groups, H corrected for ties = 7.981, $DF = 2$, $p = 0.018$). Paired comparisons of the three areas indicate that the Coast Range has significantly less decline than the other two areas (t test, $p = 0.004$ to San Joaquin Val-

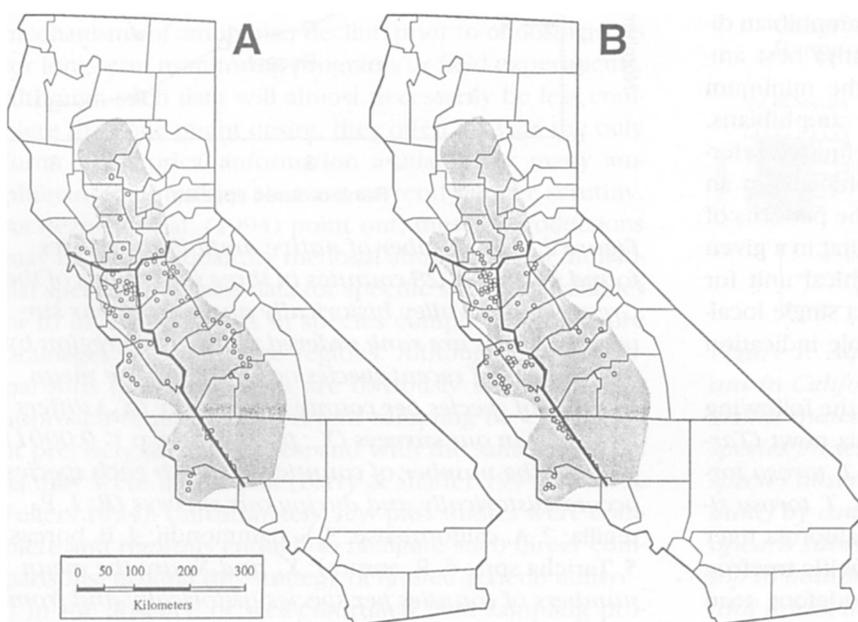


Figure 3. Historic records for *Ambystoma californiense* from the Great Central Valley (A). The present distribution of *A. californiense* in the Great Central Valley based on our surveys (B). Shaded area as in Fig. 1.

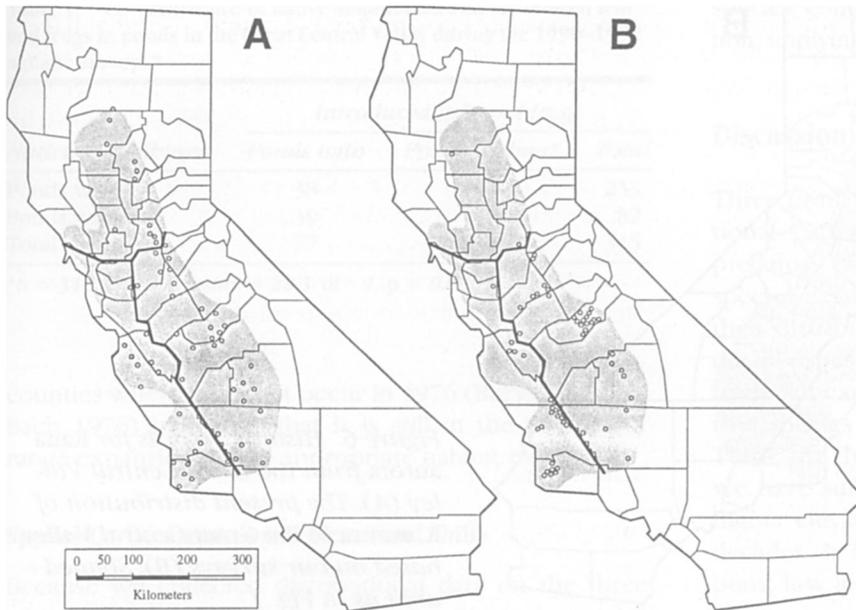


Figure 4. Historic records for *Scaphiopus hammondii* from the Great Central Valley (A). The present distribution of *S. hammondii* in the Great Central Valley based on our surveys (B). Shaded area as in Fig. 1.

ley; $p = 0.013$ to Sacramento Valley; corrected using Bonferroni method for multiple tests [Rice 1989]). However, the Sacramento and San Joaquin Valleys did not significantly differ in amount of decline ($p = 0.753$).

Although all species show some decline, they range from slight (1/28 counties lost for *P. regilla*) to extreme (24/28 counties lost for *R. aurora*) (Fig. 2B). To examine these individual species patterns in more detail, we plotted the recent and historic localities in the Great Central Valley for four native species and the bullfrog. For this analysis we plotted up to seven localities per county for the historic distributions to maintain a similar 10- to 30-km distance between localities as we did for our field survey. We also plotted all of our localities for

each species on the recent maps, for visual comparison. Figures 3-7 illustrate the historic and recent distributions of *A. californiense*, *S. hammondii*, *B. boreas*, *R. aurora*, and *R. catesbeiana*, respectively, within the Great Central Valley. We did not plot *P. regilla* or *T. torosa* because the former showed essentially no decline and the latter is only peripherally present in parts of the Sacramento and San Joaquin Valleys.

When compared with their historic distributions we see a gradient in the degree of decline across the native species. *A. californiense* (Fig. 3), which still occurs over much of its previous distribution, appears to be in the initial stages of fragmentation and decline. It is still present in most counties, although peripheral popula-

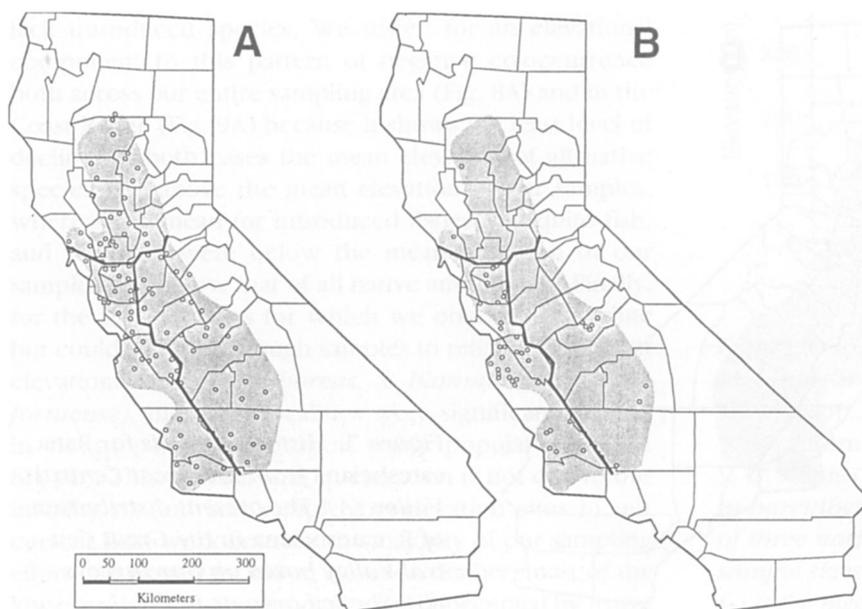


Figure 5. Historic records for *Bufo boreas* from the Great Central Valley (A). The present distribution of *B. boreas* in the Great Central Valley based on our surveys (B). Shaded area as in Fig. 1.

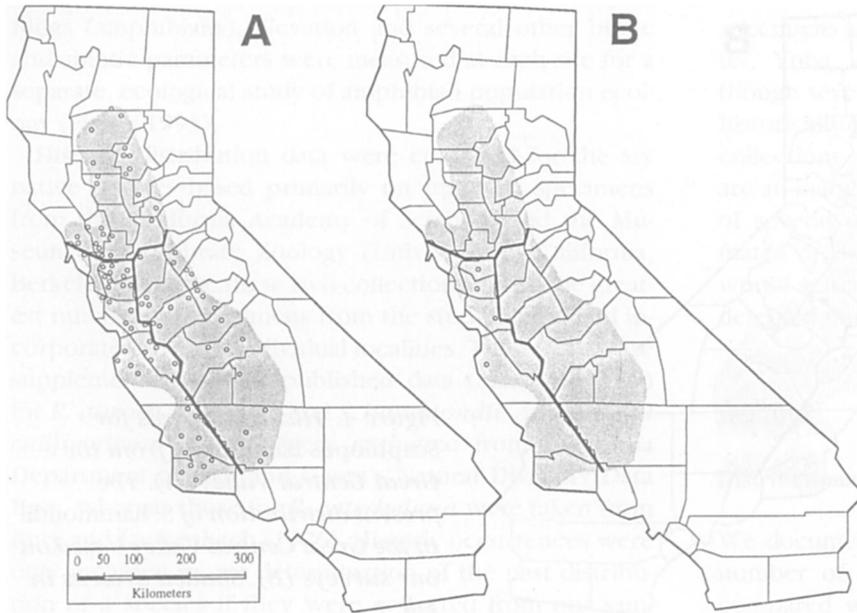


Figure 6. Historic records for *Rana aurora* from the Great Central Valley (A). The present distribution of *R. aurora* in the Great Central Valley based on our surveys (B). Shaded area as in Fig. 1.

tions in the Sacramento and eastern San Joaquin Valleys are no longer extant. *S. hammondi* (Fig. 4) shows a more severe pattern of decline with virtually complete extirpation from the Sacramento Valley, and a reduced density of populations in the eastern San Joaquin Valley. *B. boreas* (Fig. 5) shows a further continuation of this trend with virtually no recruitment during our sampling period in the Sacramento or San Joaquin Valleys, but apparently viable populations in the Coast Range. Finally, *R. aurora* (Fig. 6) is in the final stages of decline, and we found it in only a few isolated ponds in the Coast Range. Thus, at the individual species level we see a common sequence of decline in native pond-breeding amphibians

with losses occurring first (and most severely) in the Sacramento Valley, followed by the San Joaquin Valley, and finally by the Coast Range.

Changes in distribution for the introduced bullfrog are shown in Fig. 7. Historically, bullfrogs have been found throughout the Sacramento and eastern San Joaquin Valleys in permanent ponds, sloughs, and rivers, with apparently limited invasion into Coast Range habitats. Although our current sampling was often in suboptimal bullfrog habitat, we still found it abundant in ponds throughout the Sacramento Valley, but only in scattered localities in the Coast Range and San Joaquin Valley. However, we did record it for San Benito and Monterey

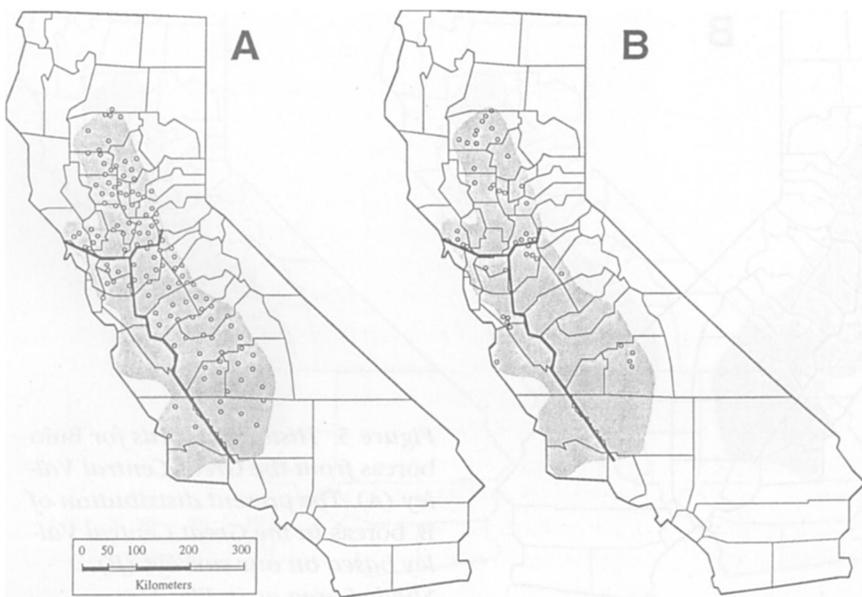


Figure 7. Historic records for *Rana catesbeiana* from the Great Central Valley (A). The present distribution of *R. catesbeiana* in the Great Central Valley based on our surveys (B). Shaded area as in Fig. 1.

Table 1. Co-occurrence of native amphibians and introduced fish and frogs in ponds in the Great Central Valley during the 1990–1992 aquatic surveys.*

Native amphibians	Introduced fish and frogs		Total
	Ponds with	Ponds without	
Ponds with	38	195	233
Ponds without	39	45	82
Total	77	238	315

*n = 315 ponds; G value = 28.3, df = 1, p < 0.0001.

counties where it did not occur in 1976 (Bury & Luckenbach 1976) indicating that it is still in the process of range expansion where appropriate habitat exists.

Species Co-Occurrences and Elevational Shifts

Because we collected distributional data on the three major groups of potential exotic predators (mosquito fish, other fish, and bullfrogs), we can examine the pattern of co-occurrence and habitat shifts of native amphibians and introduced exotics. Table 1 shows that there is a significant, inverse relationship between introduced exotics and native amphibians (G test comparing co-occurrence of all native species with all exotics, G value = 28.3, DF = 1, p < 0.0001), and this pattern holds individually for virtually all native species for which we have reasonable sample sizes (Fisher 1995). When we tested the three individual predator classes, we also found a significant, inverse relationship with native species, although the frequent co-occurrence of several introduced exotics in the same pond makes it impossible to unambiguously assess the impact of each predator class on native amphibian species. Thus, although native and introduced species do sometimes co-occur, the vast majority of ponds harboring native amphibians lack introduced species. We tested for an elevational component to this pattern of negative co-occurrence both across our entire sampling area (Fig. 8A) and in the Coast Range (Fig. 9A) because it shows the least level of decline. In both cases the mean elevation of all native species was above the mean elevation of our samples, whereas the mean for introduced fishes, mosquito fish, and bullfrogs were below the mean elevation of our samples and below that of all native amphibians. Finally, for the three species for which we observed a decline but could still find enough samples to reliably document elevational ranges (*B. boreas*, *S. hammondi*, *A. californiense*), historical localities were significantly lower in elevation than are current viable populations (Figs. 8B, 9B). This upward shift in elevation is not due to our inability to find and sample low-elevation sites in our current field work because the majority of our sampling effort was from 0 to 200 m elevation. Rather, most of the low-elevation sites we sampled were unoccupied by native

species, compared with their historical pattern of distribution, implying they have been lost from these areas.

Discussion

Three primary results stem from our analysis of distributional patterns of native amphibians and introduced predators in the Great Central Valley. First, all native species examined appear to show an overall decline in their distribution. Second, native amphibians and introduced fishes and bullfrogs tend not to co-occur, with introduced exotics occupying low-elevation sites, and native species persisting primarily at higher elevations. Third, the three species of native amphibians for which we have sufficient samples, have become restricted to higher elevations of occupied sites over the last several decades. It thus seems plausible that habitat modifications, low levels of topographic relief, or a combination

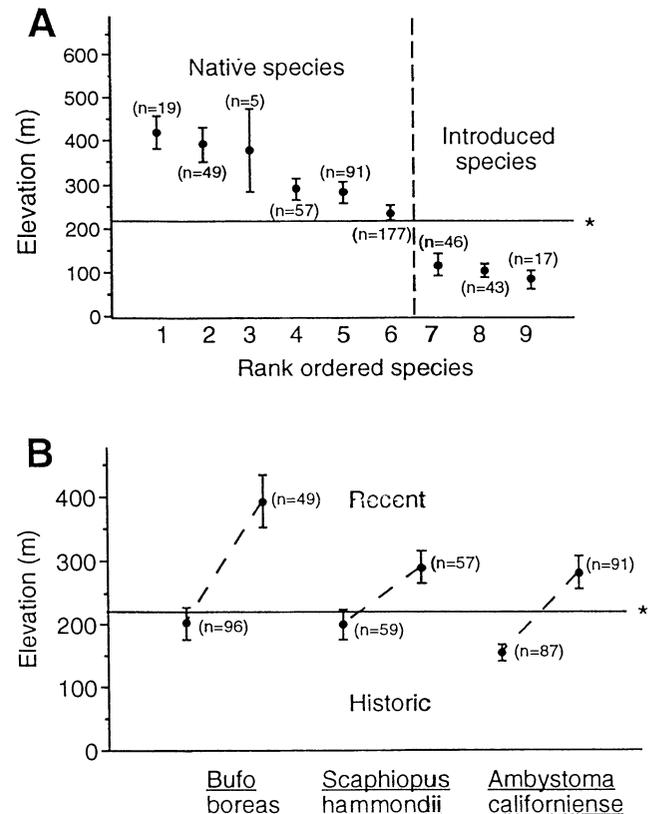


Figure 8. Current elevational distribution of native and introduced species rank ordered by elevation: 1, *Taricha* spp.; 2, *B. boreas*; 3, *R. aurora*; 4, *S. hammondi*; 5, *A. californiense*; 6, *P. regilla*; 7, *Fish*; 8, *R. catesbeiana*; 9, *G. affinis* (bars represent SE and sample sizes [n] are in parentheses) (A). Historic versus recent elevations of three native amphibians (bars represent SE and sample sizes [n] are in parentheses) (B). The asterisk (*) is the mean elevation of all 315 ponds in our survey.

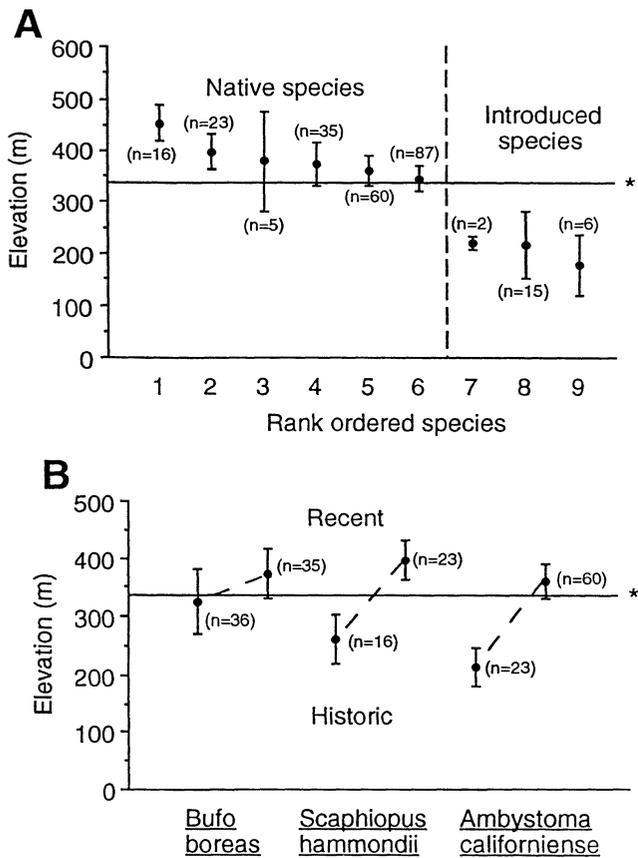


Figure 9. Current elevational distribution of native and introduced species in Coast Range only rank ordered by elevation: 1, *Taricha* spp.; 2, *S. hammondii*; 3, *R. aurora*; 4, *B. boreas*; 5, *A. californiense*; 6, *P. regilla*; 7, *G. affinis*; 8, *Fish*; 9, *R. catesbeiana* (bars represent SE and sample sizes [n] in parentheses) (A). Historic versus recent elevations of three native amphibians for the Coast Range only (bars represent SE and sample sizes [n] are in parentheses) (B). The asterisk (*) is the mean elevation of all 134 ponds in the Coast Range.

of factors have allowed exotic species to invade low-elevation sites, and this has contributed to the overall pattern of decline seen in the native amphibians.

Before examining this hypothesis in greater detail, it is important to recognize the potential limitations to our analysis. As emphasized by Reznick et al. (1994), the kind of interpretations we wish to make rely on the quality of the museum records for baseline historical data as well as our own sampling for current distributional information. Although both are subject to many sources of error, we feel they provide a reasonable basis for documenting historical patterns at the coarse scale over which we are working. Several potential sources of error have been identified in the literature, including (1) local, stochastic population fluctuations and (2) year-to-year variation in patterns of recruitment. Both of these may effect the reliability of either the museum records

or our own sampling; however, the key question is whether either will lead to a systematic bias that would be interpreted as a decline over time. Assuming that local, stochastic population fluctuations are a normal occurrence (Shaffer & Fisher unpublished data; Heyer 1979; Corn & Fogelman 1984; Pechmann et al. 1991; Dodd 1992; Hairston & Wiley 1993; Kagarise Sherman & Morton 1993), we might not record all potential species at a particular breeding site either in our current sampling or in museum records. However, unless a local extirpation (i.e., across an entire county) has occurred, we should record them at a nearby pool and still score them as regionally present historically and currently. Because we were not quantifying the numbers of individuals at each pond, even severe fluctuations will not affect our results as long as a few individuals reproduce most seasons (Trenerry et al. 1994; Hayek & Buzas in press). In addition, the size of our sampling unit (the county) ensures that we will average over small-scale fluctuations and only tally declines that encompass many hundreds to thousands of square kilometers.

The effects of yearly variation in recruitment due to widespread environmental factors are potentially more severe, especially because most localities were only sampled once during our 3-year survey. In particular, if our surveys were conducted during particularly dry years and certain species did not breed while others did, we might incorrectly interpret a lack of breeding due to low rainfall levels as a real, species-specific decline. Circumstantial evidence suggests this is not a serious concern, but may influence a few species. First, our 3 sampling years were not uniformly low-rainfall winters. If we use Davis (Yolo county, a southern Sacramento Valley site) as representative of the Great Central Valley, the 1989–1990 rainfall (1 July–30 June) was 15.85 inches (91% of the 17.27 inches 100-year average), 1990–1991 was 82% of normal, and 1991–1992 was 100% of normal. Viewed another way, of the 15 years from 1980–1981 to 1994–1995, our 3 years were ranked sixth, ninth, and eleventh wettest. Thus, although none of our sampling years had experienced extremely high rainfall, they were never so low that we would expect widespread suppression of amphibian breeding activities. Evidence from localities that we have visited several times sheds some additional light on this problem. At two localities that we visited multiple times over several years, we noted a consistent pattern of presence and absence of species regardless of yearly rainfall: *A. californiense* and *P. regilla* larvae were always present, whereas the other species were always absent. Nevertheless, at our long-term study site at the Hastings Reservation in Monterey County, H.B.S. has found that *A. californiense*, *P. regilla*, and *T. torosa* larvae are reliably present regardless of rainfall but *B. boreas* tadpoles and metamorphs fluctuate much more with rainfall patterns (Shaffer & Koenig, unpublished data). Although the data are less complete, field work in

1993–1994 and 1994–1995 by RNF in southern California (San Diego, Orange, and Riverside counties) demonstrates a similar species-specific effect: *B. boreas* and *S. hammondi* show year-to-year variation in recruitment depending on rainfall patterns, whereas *P. regilla* is a more consistent breeder across years (*Ambystoma* and *Rana* do not occur at these sites). Thus, it is possible that the relatively severe declines we observed in *B. boreas* and *S. hammondi* are in part due to reduced breeding activity associated with moderate rainfall during 1990–1992. Nevertheless, we did observe some breeding in all species in all years, which confirms that there was sufficient rainfall to induce breeding in the regions we were sampling. Finally, even if the apparent decline in some species is partially a function of rainfall patterns, it points out the inherent demographic instability in these taxa and their potential susceptibility to continual habitat modification. In particular, species that undergo large yearly fluctuations in population size may be extremely sensitive to habitat changes that interfere with recolonization success compared to species that maintain relatively constant population sizes across years (Travis 1994).

What mechanism, or set of mechanisms, might be causing amphibian declines in the Great Central Valley of California? In western North America the primary candidates identified to date are increased ultraviolet (particularly UVB) radiation (Blaustein et al. 1994a), and introduced predatory species (Moyle 1973; Hayes & Jennings 1986; Bradford 1989; Bradford et al. 1993). Although we have no data on UVB as a mechanism for decline in the Central Valley, it may be an important factor in the decline of several species in Oregon (Blaustein et al. 1994a). However, over the range of habitats we examined, declines are most severe at low elevations, where the harmful effects of UVB should be lowest. Thus, in the absence of direct evidence on ambient UVB levels, it does not appear to be a major stressor in the Great Central Valley system.

Consider the causal hypothesis that introduced species are a potential mechanism of decline, rather than a spurious correlation. Most introduced exotics are relatively recent components of the freshwater fauna of California (Moyle 1976; Moyle et al. 1982; Moyle 1986; Leidy & Fiedler 1985; Swift et al. 1993) and are concentrated at elevations below 150 m in our surveys (Fig. 8A). If introduced species have caused declines, then (1) native amphibians should currently be missing from low elevations where exotics are common, and (2) there should have been a historic restriction to higher mean elevations in the native amphibians as they are eliminated from low-elevation sites. Both of these predictions are borne out by our analysis (Table 1, Figs. 8 & 9), and it appears most strongly in the Sacramento Valley (Fig. 1). The same process may be in effect in the Coast Range (Fig. 1), although there is apparently still suffi-

cient unaffected habitat in most counties that our very conservative estimate of decline has not yet registered in this region. However, we predict that widespread declines will become apparent if exotic species continue to spread in low-elevation Coast Range habitats. A different pattern seems to be in effect in the San Joaquin Valley (Fig. 1), where we found few introduced exotics yet catastrophic amphibian declines. The San Joaquin is the most intensively farmed and most modified of the three regions. One plausible interpretation of amphibian declines here is that the few remaining valley floor ponds and pools have been so affected that they are no longer habitable even for introduced species (Ohlendorf et al. 1988; Parker & Knight 1992; Saiki et al. 1992). Thus, the only remaining habitat in the region consists of higher-elevation sites that seldom contain exotics.

Teasing apart the independent and combinatorial contributions of multiple factors, including increased UVB (Blaustein 1994) and exotics, presents a major challenge to reversing amphibian declines. For UVB there is reasonable documentation that ambient levels can cause embryonic mortality for some species (Blaustein et al. 1994a). For exotics all three introduced categories have been shown to prey on congeners of our native species either experimentally or in the field (L. Kats, personal communication; P. Trenham, personal communication; Werschkul & Christensen 1977; Hammerson 1982; Jennings & Hayes 1985; Kats et al. 1988). Unfortunately, introduced exotics tend to thrive in highly modified habitats, confounding habitat modification and degradation with the actual exotic predator as the real source of decline (Moyle 1973; Moyle 1976; Moyle et al. 1982; Leidy & Fiedler 1985; Baltz & Moyle 1993; Swift et al. 1993). However, our frequent observation of successful breeding activity by native amphibians in extremely modified breeding sites as long as they were free of exotics (Barry & Shaffer 1994; Shaffer & Fisher unpubl.) supports the interpretation that the exotic species themselves are an important element in the path to decline and local extirpation. More complex interactions may also be taking place; for example, it is possible that introduced exotic predators force egg-laying or young tadpole development to occur in shallow water where the effects of UVB are more severe.

We agree with Reznick et al. (1994) that the historical approach we have taken in this study provides a defensible, rapid method for assessing population trends over a suitable geographic scale, and we encourage others to conduct similar surveys for other large regional biotas. To date, only a handful of historical trend analyses have been conducted on amphibians in the western United States (Corn et al. 1989; Fellers & Drost 1993; Drost & Fellers 1994), and we have very little information on the patterns of historical decline or introduced species in other parts of the world (e.g., Inger & Voris 1993; Richards et al. 1993). Although many regions lack the neces-

sary museum records to document historical shifts, there are enough with reasonable, long-term collections to assess distributional shifts in community assemblages over a range of habitat types. Such analyses, in combination with ongoing research programs quantifying local population demography and experimental analyses of mechanisms, may be the best strategy to define and to begin reversing trends in amphibian declines.

Acknowledgments

We thank all those who provided assistance in the field: S. Rollmann, S. Stanley, M. Meyers, P. Ustach, J. DiDonato, A. Gluesenkamp, D. Irschick, J. King, K. Lappin, M. Littlefield, C. Austin, and S. Sweet. Historic data were supplied by J. Vindum of the California Academy of Sciences and J. Rodriguez of the Museum of Vertebrate Zoology. A. Blaustein, T. Case, M. Hellberg, R. Heyer, E. Main, R. Radtkey, T. Schoener, M. Vicario, D. Wake, H. Wilbur, and one anonymous reviewer critically read earlier versions. S. Stanley and S. Rollmann provided lab assistance. M. Jennings supplied unpublished distributional data. J. Brode, C. Brown, D. Duncan, R. Hansen, and A. Roest provided additional locality information. J. Froke, J. Grant, N. Nediff, P. Patrick, M. Stromberg, E. Tanaka, and M. Urtitia, in particular, provided access to land. The Department of Air and Water Resources (University of California, Davis) provided rainfall data. Aspects of this work were supported by the California Department of Fish and Game Inland Fisheries Division (FG 9422), the National Park Service/NBS, NSF BSR 90-18686, and the UC Davis Agricultural Experiment Station.

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