Collapse of a Regional Frog Fauna in the Yosemite Area of the California Sierra Nevada, USA

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Abstract: *There has been much concern about widespread declines among amphibians, but efforts to determine the extent and magnitude of these declines have been hampered by scarcity of comparative inventory data. We resurveyed a transect of the Sierra Nevada mountains in western North America that was carefully studied in the early 1900s. Our comparisons show that at least five of the seven frog and toad species in the area have suffered serious declines. One species has disappeared from the area entirely and a second species, formerly the most abundant amphibian in the area, has dwindled to a few small remnant populations. These declines have occurred in a relatively undisturbed, protected area and show some of the same patterns noted in other reports of amphibian declines. Introduced predatory fish, possibly interacting with drought-induced loss of refuge habitats, have contributed to the decline of some species. However, the overall cause of these dramatic losses remains unknown.*

El colapso de la fauna regional de bactracios en el área de Yosemite en la Sierra Nevada de California (EEUU)

Resumen: *Ha existido mucha preoccupación acerca de las declinaciones generalizadas entre anfibios, pero los esfuerzos para determinar el alcance y magnitud de estas declinaciones han sido limitados por la escasez de registros de datos comparativos. En el presente estudio reevaluamos una transecta de las montañas de la Sierra Nevada, en el oeste de Norte America, que fue estudiada cuidadosamente a principios del 1900. Nuestras comparaciones muestran que por lo menos cinco de las siete especies de ranas y sapos en el área han sufrido serias declinaciones. Una especie ha desaparecido totalmente del área y una segunda especie, que era el anfibio mas abundante en el área, se ha reducido a unas pocas poblaciones remanentes. Estas declinaciones han ocurrido en áreas relativamente protegidas y poco perturbadas, y muestran algunos de los mismos patrones evidenciados en otros reportes sobre la declinación de anfibios. Los pecos predadores introducidos, que posiblemente interactuen con la pérdida de habitat para refugio debido a las sequias, han contribuído a la declinación de algunas especies. Sin embargo, las causas generales de estas dramáticas pérdidas continuan siendo ignoradas.*

Introduction

Historically, amphibians have not received the conservation concern accorded groups such as birds and large mammals. This may be due, in part, to less popular interest in amphibians, but it is also due to poor knowledge of population processes and trends for most amphibian species. In the last few years there has been increased concern about amphibians following reports of population declines in frog and toad species in many areas of the world (Barinaga 1990; Blaustein & Wake 1990a; Tyler 1991; Vial & Saylor 1993; Wake 1991; Wyman 1990). Recent compilations (such as Vial & Saylor 1993) note that many declines are clearly linked to habitat loss or degradation. Other losses do not have obvious explanations, but some tentative patterns have emerged: 1) reported declines have been mainly or entirely among

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Paper submitted August 26, 1994; revised manuscript accepted July 13, 1995.

anuran species (frogs and toads); 2) certain taxa and geographic areas seem to be more affected than others (in western North America, for example, most reports have concerned frogs of the genus *Rana* and true toads, genus *Bufo*; Corn, in press; Hayes & Jennings 1986; Vial & Saylor 1993); 3) many of the reported declines have been among high-elevation species (Wake 1991); 4) some declines and losses have been among species with restricted geographic and habitat ranges or among populations of more widely distributed species at the edge of their range (Fellers & Drost 1993; Pounds & Crump 1994); and 5) the declines appear to be recent, with well-documented declines and local or regional disappearance of species within the last 20 years (Bradford et al. 1994; Carey 1993; Pounds & Crump 1994).

Several western North American anurans are among those that have suffered serious, unexplained losses. Two species with restricted ranges, *Bufo hemiophrys baxteri* (the Wyoming toad) and *Rana onca* (relict leopard frog), are close to extinction (Corn, in press). Formerly widespread and abundant species have also been affected: Dramatic losses have occurred in *B. boreas* (the western toad) in the Rocky Mountains (Carey 1993; Corn et al. 1989) and repeated reproductive failures have been reported in the Pacific Northwest (Blaustein & Olson 1991; Blaustein et al. 1994). Populations of *R. muscosa* (the mountain yellow-legged frog) have disappeared from over 75% of study sites they formerly inhabited in the mountains of California (Bradford et al. 1994). *Rana aurora* (the red-legged frog) has disappeared or declined over much of its range in California (Hayes & Jennings 1986; Moyle 1973), and declines in *R. pipiens* (the northern leopard frog) have been reported across the species' range in the western U. S. and Canada (Clarkson & Rorabaugh 1989; Corn, in press; Hayes & Jennings 1986; Bishop & Petit 1992).

Many authors have noted the paucity or poor quality of comparative information (Barinaga 1990; Vial & Saylor 1993). There are, however, some overlooked sources of baseline data on amphibian populations in the western United States. These include an intensive survey of vertebrate populations in the Sierra Nevada mountains of California, conducted in 1915–1919 by zoologists Joseph Grinnell and Tracy Storer (Grinnell & Storer 1924). There have been reports of amphibian declines in the Sierra Nevada region (Bradford et al. 1994; Hayes & Jennings 1986; Moyle 1973), and the Grinnell and Storer survey offered a unique opportunity to evaluate long-term trends in several amphibian populations. Our objectives in this study were to 1) evaluate changes in amphibian distribution and abundance over a large region encompassing different habitats and a variety of amphibian species; 2) investigate possible causes for observed changes; and 3) assess patterns in population and community changes, particularly as they relate to amphibian declines in other areas.

Study Area and Amphibian Fauna

Grinnell and Storer (1924) studied the distribution and ecology of vertebrate animals along a transect through the Sierra Nevada mountains in California, USA. Their 144-km long transect extended from the edge of the California Central Valley, over the crest of the Sierra Nevada mountains to Mono Lake on the western edge of the Great Basin desert (Fig. 1). Forty sampling sites along the transect ranged in elevation from 75 m at Snelling to 4000 m on Mt. Lyell. These sampling sites included a wide variety of habitats, from oak-pine savanna at the west end, through montane forest (*Abies - Pinus*), to alpine meadows and tundra along the broad crest of the mountains, to sagebrush steppe (*Agropyron - Artemisia*) in the high desert around Mono Lake. Amphibian habitats included river backwaters at the low elevations, small ponds, lakes, mountain streams, wet meadows, and ephemeral pools.

Grinnell and Storer conducted most of their field work in the spring and summer of 1915, with additional observations in 1919. They recorded seven amphibian species throughout the study area, including three ranid frogs, *Rana aurora*, *R. boylii* (foothill yellow-legged frog), and *R. muscosa*; two toads, *Bufo boreas* and *B. canorus* (Yosemite toad); one spadefoot toad, *Scaphiopus intermontanus* (Great Basin spadefoot); and one treefrog, *Hyla regilla* (Pacific treefrog).

Methods

We studied Grinnell and Storer's final report (Grinnell & Storer 1924) and the original field notes of all of the survey participants (field notes of Grinnell, Charles L. Camp, Joseph Dixon, Gordon Ferris, Charles D. Hollinger, Walter P. Taylor, and Donald D. McLean are maintained at the Museum of Vertebrate Zoology, University of California, Berkeley; Storer's field notes are at the California Academy of Sciences, San Francisco, California). We recorded and tabulated their observations, which provided information on distribution and abundance of amphibians, as well as on seasonal activity, habitat use, and reproduction. From their maps and descriptions, we noted the exact sites they visited.

Grinnell and Storer typically recorded only relative abundance of amphibian species; they generally did not report counts or numerical estimates of abundance. For this reason, our evaluation of changes in abundance was limited to comparing abundance categories (such as rare, common, abundant). Based on comments in field notes (where some numerical estimates were provided) and on information such as numbers of specimens collected, we used the following abundance classes to categorize counts: <10 per site = rare; 10–30 per site = common; >30 per site = abundant.

We reviewed museum records from the Museum of Vertebrate Zoology and the California Academy of Sciences to locate additional site records for amphibians along the Yosemite transect. We also noted ponds, streams, and meadows from maps, aerial photos, and field observations that appeared to provide suitable habitat for amphibians. We searched these additional sites (not covered by Grinnell and Storer and hereafter referred to as "non-GS sites") to add to the extent of our survey and to provide additional information on pattern and timing of population changes observed.

To duplicate the earlier surveys as closely as possible and provide a valid basis for comparisons, we defined sample sites based on the written accounts or notes of the Grinnell and Storer team or the notes accompanying museum specimens. For this reason our sample sites ranged from specific, relatively small areas (such as Evelyn Lake) to larger, less well-defined areas (such as Sweetwater Creek, 3 km southeast of Feliciana Mountain). When the earlier area description was not precise, we searched a larger area to cover the limits of the general site description. In some instances the Grinnell and Storer survey members moved about extensively. In these cases we noted specific locations where they reported amphibians and defined these locations as the survey sites.

Between 11 May and 11 September, 1992, we visited all of Grinnell and Storer's collecting sites that we could accurately locate (38 out of 40; hereafter referred to as "GS sites"). During the course of the late spring and summer,

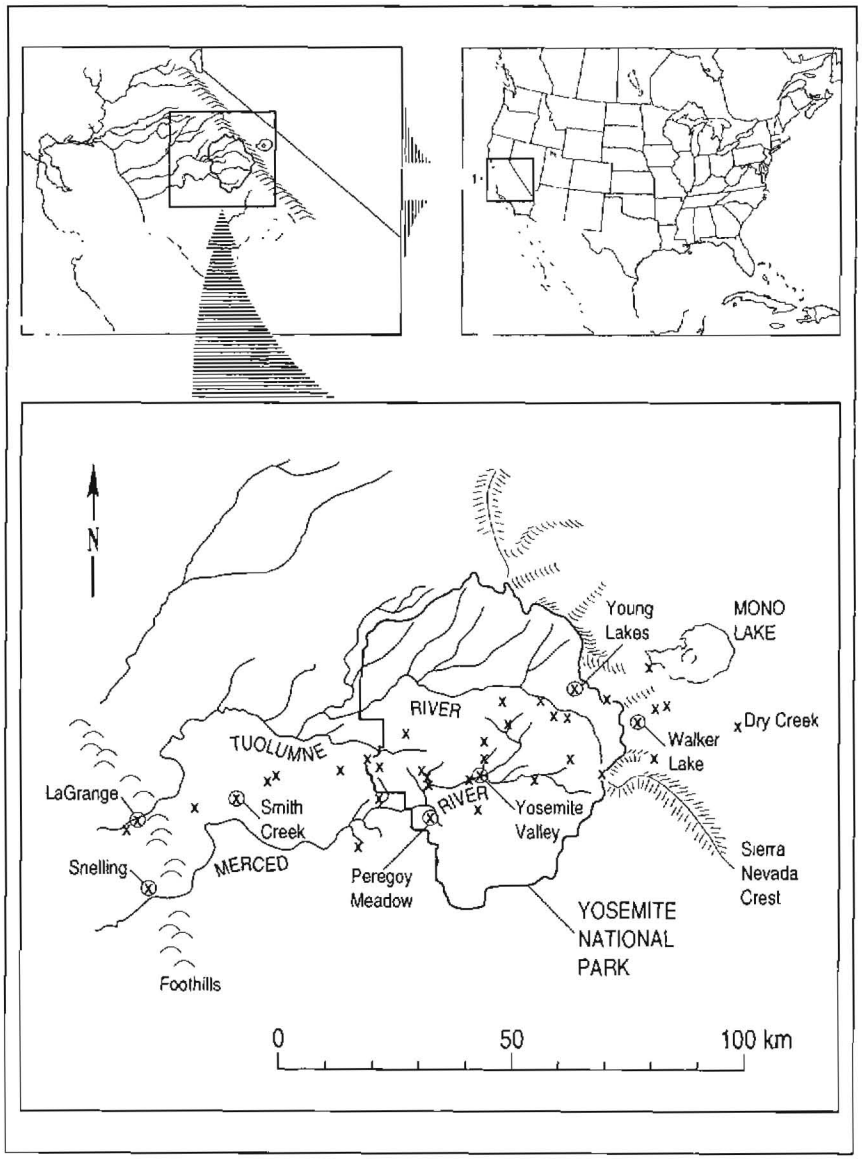

Figure 1. Map of the Yosemite area of the California Sierra Nevada showing areas sampled in 1992 and 1993 during a survey of amphibian distribution and population status. Sites visited ranged from low foothills in the west, across the Sierra Nevada crest, to the vicinity of Mono Lake on the east.

we spent a total of 44 person-days surveying for amphibians. During the early part of this period we followed the amphibian breeding season at the different elevations, checking the lowest areas first and moving to higher elevations as the snow and ice melted. At each site one or both of us thoroughly searched all aquatic habitats suitable for anurans. At some pond and meadow sites we stayed into the evening to listen for calling frogs and toads.

We used visual encounter surveys (Crump & Scott 1994; Fellers & Freel 1995), walking back and forth across meadow areas and making thorough searches of the margins of streams, lakes, and ponds. In meadows we looked for all areas of standing water and made a careful search of these either by wading through the area or by walking the circumference of larger, deeper bodies of water. Around potholes, ponds, and lakes we looked for adult frogs sitting along the shore or in the shallows and scanned the near-shore waters for tadpoles. In water that was turbid or had extensive aquatic vegetation, we used long-handled nets to sweep for tadpoles. Tadpoles of all species could be reliably identified in the field and were generally easy to find in areas where they occurred. Because we thoroughly searched all sites for tadpoles, this provided corroboration of presence or absence of different species, as well as reflecting reproductive effort. One of the species in the survey area, *Scaphiopus intermontanus*, visits aquatic breeding sites for relatively brief periods of time and then retreats to terrestrial habitats where it is difficult to locate. Presence and abundance of tadpoles potentially provided the best indication of the distribution and numbers of this species.

Because of the nature of the respective studies, our surveys in 1992 were more intensive than those of Grinnell and Storer. We thoroughly searched areas specifically for amphibians, and noted all amphibian life stages (eggs, larvae, and adults). The Grinnell and Storer team conducted general surveys for all vertebrate species; in some instances they took time to search specifically for amphibians, but in general they simply noted amphibians as they encountered them. They rarely noted tadpoles or egg masses, and in some instances they only referred briefly to species that were obviously abundant. Also, in cases where the location of a GS site was imprecise, we purposely searched a larger area to be sure we included their survey site. For these reasons indications of decline in our data should be conservative; we may have located small populations that Grinnell and Storer overlooked or failed to record. Indications of increase from our surveys may be overstated for the same reason.

Results

Nearly all anuran species along the Yosemite transect showed a strong downward trend between 1915/1919 and 1992. Local populations had disappeared at many of the GS sites, and we found few or no new populations at sites where Grinnell and Storer had not found them (Table 1). Overall, most of the native frog and toad species were present at far fewer survey sites in 1992 than in 1915. Three species (*Rana aurora, R. boylii*, and *Scaphiopus intermontanus*) were not found at any of the GS sites in 1992. Formerly widespread *Bufo boreas* and *R. muscosa* were reduced to one site and two sites, respectively. Only *Hyla regilla* was found at a comparable number of sites between the two survey periods. *R. catesbeiana*, the introduced bullfrog, had not invaded the area at the time of the Grinnell and Storer survey; it was present at four of the survey sites in 1992.

Extensive areas were searched in addition to the GS sites, particularly in the higher elevation habitats. Non-GS sites were larger areas, including meadow com-

Table 1. Anuran populations found by Grinnell and Storer (1924) during their original survey of a transect across the Sierra Nevada mountains through Yosemite National Park compared to populations found in 1992.

Species	*No. Sites*[a] *1915*	*Still present*[b] *1992*	*New sites*[c] *1992*
Bufo boreas	8	1	0
Bufo canorus	13	7	0
Hyla regilla	22	16	3
Rana aurora	3	0	0
Rana boylii	7	0	0
Rana muscosa	14	2	0
Rana catesbeiana	0	0	4
Scaphiopus intermontanus	3	0	0

[a] *Number of Grinnell and Storer's sampling sites at which they found the species.*
[b] *Number of Grinnell and Storer sites where the species still present in 1992.*
[c] *Number of sites where the species was found in 1992 but was not reported in 1915.*

Table 2. Amphibian occurrence at additional sites[a] searched in a survey of the Sierra Nevada mountains through Yosemite National Park in 1992 and 1993.

Species	*No. of Sites*[b]	*Species Present*
Bufo boreas	6	1
Bufo canorus	15	1
Hyla regilla	22	12
Rana aurora	7	1
Rana boylii	10	0
Rana catesbeiana	7	4
Rana muscosa	17	3
Scaphiopus intermontanus	2	0

[a] *These sites were not reported on by the Grinnell and Storer (1924) survey of the same transect.*
[b] *Number of sites listed for each species denotes Sites searched within the species' distributional range that had suitable habitat for that species.*

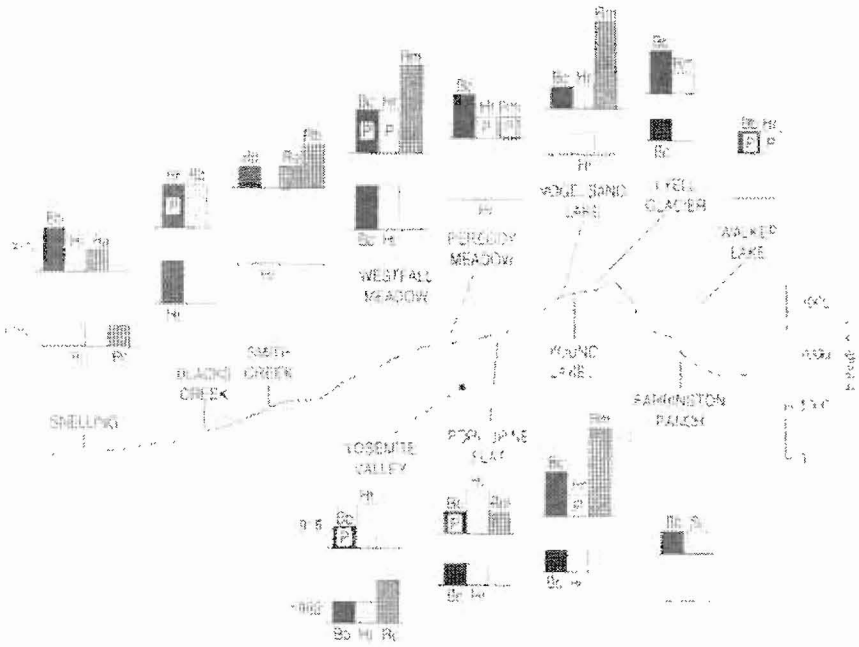

Figure 2. Comparison of local amphibian communities at selected sites in the Yosemite area of California between 1915 and 1992. Corresponding graphs for each named site show amphibian occurrence and relative abundance in 1915 (top) and 1992 (bottom). Short, medium, and tall bars denote rare, common, and abundant, respectively. The P *in some 1915 graphs means the species was noted as present, but no information was provided on relative abundance.* Bb = Bufo boreas; Bc = B. canorus; Hr = Hyla regilla; Ra = Rana aurora; Rb = R. boylii; Rc = R. catesbeiana; Rm = R. muscosa; St = Scaphiopus intermontanus. *Shading differences are provided for contrast only.*

plexes, marshes, stream courses, and clusters of lakes and ponds. Except for *H. regilla* and *R. catesbeiana*, none of the species were common at non-GS sites, even though many areas of apparently suitable habitat for each species were searched (Table 2).

For 12 of the GS sites we found good information on relative abundance at the time of the earlier survey. We made a site-by-site comparison of abundance for all species at these sites in 1915 and 1992. Where native amphibians persisted, they showed declines in numbers at most sites (Fig. 2).

Individual Species

BUFO BOREAS (WESTERN TOAD)

Grinnell and Storer noted *B. boreas* as a common resident below 1360 m on the west side of the Sierra Nevada, occurring also at Walker Creek on the east slope. They described the species as "exceedingly abundant" at most localities in the western foothills (Grinnell & Storer 1924; 655-656). In the 1992 survey we found small numbers of *B. boreas* at only one of the six sites where Grinnell and Storer recorded them. At this site (Yosemite Valley) we found two adult females (one dead of unknown causes) and two groups of 20 and 30 tadpoles.

BUFO CANORUS (YOSEMITE TOAD)

Grinnell and Storer recorded *B. canorus* in meadows and around lakes and streams throughout the higher elevations, from 2040 m to 3350 m. We found this species at just over half of the sites where Grinnell and Storer found it, but in low numbers at most sites. For all of the areas surveyed, we recorded only 15 postmetamorphic *B. canorus*; only 3 of these were adults. *B. canorus* numbers were lower in at least 3 of the sites where they were still found, so that the species has declined or disappeared from at least 9 of the 13 GS sites (69%).

HYLA REGILLA (PACIFIC TREEFROG)

Grinnell and Storer recorded *H. regilla* throughout the Yosemite section, from Snelling at the edge of the Central Valley east to Walker Lake on the east side of the mountains, and up to 3230 m along the crest of the mountains. Perhaps because of its ubiquitous occurrence, Grinnell and Storer provided less detail for *H. regilla* than for other species, primarily describing unusual situations such as frogs calling from beneath melting ice and snow at high mountain lakes. At specific sites they described the species in terms ranging from "several" heard at Pleasant Valley (Storer field notes, May 1915), to "common" in the Porcupine Flat area (Storer field notes, June 1915), and "numerous" near Merced Lake (Taylor field notes, August 1915). *H. regilla* was similarly widely distributed in the 1992 survey, except that we did not find the species at any of the sites east of the Sierra Nevada crest.

Of the 22 sites where Grinnell and Storer reported *H. regilla*, we found it at 16. We also found treefrogs at Hazel Green, McCarthy Ranch, and Tioga Pass, where they

were not reported by Grinnell and Storer. We suspect the earlier survey may not have searched intensively at these latter sites or simply did not record frogs at all of the sites where they were seen. However, we conservatively record these three areas as "new" sites, so the total number of sites with treefrogs was 19 in 1992 (Table 1).

At half of the sites where *H. regilla* was present there was either no discernible change in abundance, or we were unable to judge because of insufficient information in Grinnell and Storer's notes. There was a clear decline in relative numbers at 11 of the 14 remaining areas. We divided the data for *H. regilla* into low-elevation sites (<1500 m, up to and including Yosemite Valley) and high elevation sites (>1500 m, Merced Grove and above) to assess whether population trends differed with respect to elevation (Table 3). There was no apparent trend at the 9 low elevation sites, with approximately equal numbers of increases and decreases between 1915 and 1992. At the 16 high elevation sites there was a significant trend ($p = 0.02$, Sign Test) toward decreased populations, with declines from 1915 to 1992 at all sites except one.

RANA AURORA (RED-LEGGED FROG)

Grinnell and Storer found *R. aurora* at three stream sites in the Sierra foothills. We did not find this species at any of the GS sites. In searches of the general transect area (away from specific sites surveyed by Grinnell and Storer) we located a group of *R. aurora* tadpoles in a small tributary of the Tuolumne River north of Coulterville. We did not find the species anywhere else along the transect.

RANA BOYLII (FOOTHILL YELLOW-LEGGED FROG)

Grinnell and Storer found *R. boylii* at their sites throughout the western foothill portion of the transect. Although the Grinnell and Storer survey did not find this species within the boundaries of Yosemite National Park, later observations and collections established its presence along Eleanor Creek at the base of Lake Eleanor dam, at Fern Springs within Yosemite Valley, and at Wawona (Martin 1940; Richards 1958; all of these are non-GS sites). Descriptions in Grinnell and Storer (1924) and the field notes of the Grinnell and Storer team indicate that *R. boylii* was formerly common. Specific references include "fairly common" along Smith Creek (Storer field notes, June 1915), "moderate numbers" along Blacks Creek (Storer field notes, May 1919), and "several" along Piney Creek (Camp field notes, May 1915). In spite of thorough searches for tadpoles and adults, we did not find *R. boylii* at any of the sites where Grinnell and Storer found the species. In 1992 and again in 1993 we searched other streams that offered suitable habitat in the appropriate elevational range. These sites included additional areas where *R. boylii* had been recorded in the past, including the sites within Yosemite National Park noted above and sites where a 1924 survey found the species in tributaries of the Merced River below El Portal (J. R. Slevin/Lyell Canyon Expedition collections, California Academy of Sciences). We did not find *R. boylii* at any of these sites (Table 2).

RANA MUSCOSA (MOUNTAIN YELLOW-LEGGED FROG)

At the time of the 1915 survey, *R. muscosa* was described by Grinnell and Storer (1924) as the most abundant amphibian throughout the high-elevation portion of the Yosemite transect. Their field notes describe "hundreds of frogs" at Young Lake (Camp field notes, July 1915) and "very numerous" at Westfall Meadow (Camp field notes, June 1915). In 1992 *R. muscosa* had nearly disappeared from the transect sites. We only found the species at two of Grinnell and Storer's locations: At Mono Meadow a single tadpole was captured in a dip net; and at Evelyn Lake a single adult female was captured on two separate dates along the outflow stream of the lake (presumably the same individual, distinctively marked and caught in the same general area on both dates). We found no adults, tadpoles, or eggs at any of the other GS sites. We found *R. muscosa* at a few non-GS sites. These were 1) a single adult male at the "G7" meadow along the Glacier Point Road; 2) a small population at Summit Meadow along the Glacier Point Road, where 16–18 adults and 30 tadpoles were counted in June 1992; and 3) 113 tadpoles in an isolated, glacial tarn at 3070 m elevation at Mount Hoffmann.

RANA CATESBEIANA (BULLFROG)

R. catesbeiana was introduced into the San Francisco Bay area of California in the late 1800's from eastern and

Table 3. Comparison of relative abundance of *Hyla regilla* at low elevation (<1500 m) and high elevation (≥1500 m) sites along a transect of the Sierra Nevada through Yosemite National Park between 1915 (Grinnell and Storer 1924) and 1992.[a]

	No. Sites	*Decrease*	*Increase*	*No. change*	*p-value*[b]
Low elevation	9	3	2	4	.50
High elevation	16	8	1	7	.02
Total	25	11	3	11	.03

[a] *Table entries are the number of survey sites showing decrease, increase, or no discernible change between the two survey periods. Sites where there was not a definite, conspicuous change are listed in the "No change" category.*
[b] *P-values are based on a sign test.*

central North America (Jennings & Hayes 1985) and has subsequently spread or been released into other areas around the state. It apparently had not reached the survey area by 1919, as it is a conspicuous species and was not reported by Grinnell and Storer (see also Storer 1925). In 1992 *R. catesbeiana* was common in ponds and river backwaters in foothill sites at the west end of the transect, including LaGrange, Snelling, and McCarthy Ranch. The species was also present in moderate numbers in Yosemite Valley.

SCAPHIOPUS INTERMONTANUS (GREAT BASIN SPADEFOOT)

S. intermontanus ranges into the western part of the survey area, where Grinnell and Storer found it at three high desert sites near Mono Lake. We did not find *Scaphiopus* at any of the GS sites nor anywhere else in the survey area.

Discussion

All native anuran species in the Yosemite area have experienced declines or losses of local populations since the Grinnell and Storer survey in 1915–1919 (Fig. 2). For most species our data indicate severe declines over the entire survey area. Documentation of an entire frog fauna declining in a large, diverse region is unprecedented; most previous reports of frog declines have focused on individual species or groups of species or more limited areas. Amphibians are important components of local ecosystems, and their loss may affect other species (Blaustein & Wake 1990). In the Sierra Nevada loss of *R. muscosa* from high-elevation lakes and streams has been correlated with significantly lower numbers of one of the frog's predators, the garter snake *Thamnophis elegans* (Jennings et al. 1992).

As noted by Corn (in press), a species that is undergoing a broad scale decline will show loss of historic populations, but little or no colonization of new sites. If a species is not found at historic sites, but is found at many previously unrecorded sites, then the overall trend for the species is unclear. Surveys of the non-GS sites corroborate our site-by-site comparisons with the Grinnell and Storer survey. With the exception of *Hyla regilla* and the introduced *R. catesbeiana*, very few anuran populations were found in suitable habitat at non-GS sites (Table 2). The declines we describe have occurred on a broad scale, across the entire survey area.

Declines have been most severe among the ranid frogs. Taken together, the two yellow-legged frog species were described by Grinnell and Storer as "the commonest amphibian in most parts of the Yosemite section . . . numbers, especially at the higher altitudes, far exceed those of [*H. regilla*]." *Rana boylii* has now disappeared from the transect area entirely, and *R. muscosa* has gone from being the most abundant species to one of the rarest.

Declines of the two yellow-legged frog species have apparently been recent. Moyle (1973) found *R. boylii* at 30 of 95 sites sampled in the southern and central Sierra Nevada foothills (from the Yosemite area south), but believed the species was declining at that time. In the mid-1980s, David Graber intensively searched 15 different stream reaches in the southern Sierra Nevada where *R. boylii* had formerly occurred, but failed to find the species in any of the areas (D. Graber, Sequoia National Park, pers. comm.). More recent surveys (GMF, in progress) confirm that *R. boylii* has been essentially extirpated in the southern Sierra Nevada. Likewise, local populations of *R. muscosa* in the Yosemite area have disappeared in the last 20–30 years (Maul Lake, R. Knapp, pers. comm.; Medlicott Dome and Young Lakes, GMF, unpubl. data; Westfall Meadows, Yoon 1977). Bradford et al. (1994) document the apparent extirpation of this species since 1978 throughout two drainage basin areas in Sequoia National Park in the southern Sierra Nevada (a total of 27 sites) and loss of the species at approximately half of previously known sites throughout the park in the last 30 years.

Rana aurora is no longer present at the three sites where Grinnell and Storer found it; we only found this species at a single non-GS site. Moyle (1973) likewise could only find one recent record of *R. aurora* throughout the Sierra Nevada foothills and adjacent Central Valley. This species has declined throughout much of its California range (Hayes & Jennings 1986; Moyle 1973) and has been proposed for listing under the U.S. Endangered Species Act.

The very low numbers of both *Bufo boreas* and *B. canorus* over the entire course of the active season, together with low numbers of eggs and tadpoles at the few breeding sites encountered, indicate that both species have experienced serious declines. Large declines of *B. boreas* have been reported from the Rocky Mountains (Carey 1993; Corn et al. 1989; Vial & Saylor 1993), but this is the first report of a decline for the Sierra Nevada area. The declines we describe for *B. canorus* parallel trends reported for other areas in the central and southern Sierra Nevada, where there are indications of general decline over the last 10–20 years (Bradford & Gordon 1992; Kagarise Sherman & Morton 1993).

Our surveys only included a small number of sites for *Scaphiopus intermontanus*. This species is secretive, spending much of its time underground in its desert habitat. Roland Knapp (pers. comm. 1994) found a breeding congregation of *S. intermontanus* a few kilometers east of the east end of our survey area, so the species still occurs in the vicinity. Little information is available on populations in other parts of this species' extensive range; we know of one other report of a decline in *S. intermontanus* (Orchard 1992), apparently due to habitat

destruction, but further work is needed to evaluate population trends within this species.

Hyla regilla is relatively common and widespread across its range; our data indicating a decline of this ubiquitous species are unprecedented. In addition to our site-by-site comparisons there were other indications that *H. regilla* populations are faring poorly. Several areas of apparently suitable habitat along the Yosemite transect had very few frogs. We searched the large meadow areas at Crane Flat on three occasions, but found no adult frogs nor tadpoles. Likewise, large areas of wet meadow in Yosemite Valley, Tuolumne Meadows, Tioga Pass, and other areas had many apparently suitable pools and marshes for breeding, but were nearly devoid of *H. regilla*. Isolated pools had tadpoles ranging in number from less than 100 to 200–300. Furthermore, we heard few breeding choruses of this species. During 44 person-days of fieldwork (including 17 evenings spent listening for frog choruses), we heard small numbers of calling frogs on only seven occasions.

Patterns of Decline

The amphibian declines in the Yosemite area are pervasive; serious losses were seen both among species at the edge of their range (*R. boylii, R. aurora*) and among species in the heart of their geographic distribution (*B. canorus, R. muscosa*). Both high- and low-elevation species were affected, including closely related species pairs occurring at upper and lower elevations (*B. canorus* and *B. boreas, R. muscosa* and *R. boylii*, Fig. 2). The one indication of differential effects at high elevation was seen in *H. regilla*, the only species that occurred throughout the elevational range of the transect (Table 3).

The taxonomic pattern of the Yosemite declines follows previously suggested trends. Corn (in press) and Vial and Saylor (1993) noted that ranid frogs and toads have suffered the most severe losses in western North America. In the Yosemite region the three ranid species have nearly disappeared from the entire survey area. The two *Bufo* species have also disappeared or declined at many sites, but appear to be persisting over a larger part of their original ranges. *Hyla regilla* populations appear to have changed the least. Life history patterns are correlated with taxonomic patterns, ranging from the ranid frogs, closely associated with waters of lakes and streams, to bufonids, adapted to relatively dry conditions and breeding in temporary ponds and wet meadows, to the one hylid species, which occurs in a variety of habitats and breeds in a similarly wide range of water bodies.

Community trends were similar across the length of the transect (Fig. 2). Most sites have been reduced from two or three species per site to a single species, in most cases *H. regilla*. The only significant deviation from this trend was at some of the western foothill sites, which now have introduced *R. catesbeiana* in addition to *H. regilla*. The similarity across sites was due to the loss or reduction of different species in different areas. At lower elevations *R. boylii* and *R. aurora* disappeared from stream habitats, and *B. boreas* was lost from ponds and wet meadows. At high elevations *B. canorus* and *R. muscosa* were lost or experienced marked declines in numbers. *Hyla regilla* was (and remains) the only species distributed through most of the transect area.

Possible Causes of Decline

Most amphibian declines have been recognized only after they have occurred, making it difficult to determine cause. Even where populations have been observed in the midst of decline, it has been difficult to clearly determine the factors responsible for the losses (Carey 1993; Pounds & Crump 1994). We do not know whether amphibian losses in the Yosemite region have been due to mortality or failure of recruitment, nor do we have detailed information on the timing of the declines. Close monitoring of remaining populations may be particularly important in determining the cause of the losses. Nevertheless, the extent of the decline, both geographically and taxonomically, suggests a pervasive force or forces affecting the anuran fauna in the Yosemite region, and we evaluated possible causes of decline in that light.

HABITAT LOSS AND CHANGE

A variety of hypotheses have been set forth for worldwide amphibian declines (see Blaustein & Wake 1990 and Wyman 1990 for reviews), but some of these can reasonably be discounted for the Yosemite area. Most of the sites in the survey area have been protected from habitat loss or evident habitat degradation, particularly within Yosemite National Park. Visual comparison of some of the survey sites with habitat photos from the Grinnell and Storer survey showed no apparent change in major habitat features at these sites. In particular, we saw little indication of degradation of the streams, ponds, lakes, and wet meadows that provide extensive breeding habitat for the amphibians in the transect area.

ACID PRECIPITATION

Although they do not yet show chronic acidification, high-elevation lakes in the Sierra Nevada may become temporarily acidified during spring snowmelt and following summer thunderstorms. Mean pH values measured for precipitation in the Sierra Nevada range from 5.2 to 5.5 (California Air Resources Board 1988). This is sufficient to kill sensitive zooplankton and aquatic macroinvertebrates, but does not appear to have caused

broad scale effects on the distribution of these species (Melack & Stoddard 1991). Laboratory tests indicate Sierran frogs do not suffer significant increased mortality until pH drops below 4.7 (Bradford & Gordon 1992). In a field study of lakes throughout the Sierra Nevada Bradford and Gordon (1992) found no significant relationship between pH, water chemistry, and amphibian distribution. They concluded that acid deposition was unlikely to be the cause of amphibian declines in the Sierra Nevada.

CHEMICAL POLLUTION

Insecticides and other toxic chemicals may kill or otherwise harm adult and larval amphibians (Bishop 1992; Johnson & Prine 1976; Porter & Hakanson 1976). Direct introduction of chemical pollutants is not a significant problem in the vicinity of the Yosemite transect; however, a potential indirect source of toxic chemicals is broad-scale pesticide drift from the intense agriculture practiced in the San Joaquin Valley west of the Sierra Nevada. Recent studies (Zabik & Seiber 1993) have shown that organophosphate insecticides used in the valley are transported in measurable quantities to over 1900 m in the mountains, with heaviest concentrations during winter rains. There has been little study of direct and indirect effects of many agricultural chemicals on amphibians (Bishop 1992); no specific data have been collected for amphibians in the Yosemite area, so chemical contaminants remain a potential factor in the declines.

INTRODUCED FISH

At least two factors, introduced predatory fish and drought, have had effects on some amphibians in the Yosemite region. Field (Brönmark & Edenhamn 1994; Cory 1963; Heyer et al. 1975; Kats et al. 1988) and experimental studies (Semlitsch 1993; Sexton & Phillips 1986) have found significant effects of fish predators on a variety of amphibian species, ranging from behavioral responses among adult and larval amphibians to reduction or elimination of amphibian populations following introductions of fish. Before local residents began stocking trout in lakes and streams, the waters above about 1500 m in the Yosemite area of the Sierra Nevada did not support any fish because of the effects of glaciation; native fish were blocked from ascending streams above this elevation by high waterfalls in glacial valleys. Limited stocking of trout in Yosemite National Park waters dates back to at least 1877; intensive stocking, involving thousands of fish and repeated yearly introductions, began in most areas in the 1920s (Elliot and Loughlin 1995).

Previous studies in this area of the Sierra Nevada, including the Grinnell and Storer survey, noted that frogs were essentially absent from water bodies with introduced fish (see also Cory 1963; Hayes & Jennings 1986). Using sites for which we had comparative records, we examined changes in amphibian occurrence between 1915 and 1992 in relation to fish stocking (Table 4). Intensive stocking at most of these sites (eight of nine) began after the Grinnell and Storer survey. In 1992 *R. muscosa* was absent from all seven of the sites where it was found in 1915. *Bufo canorus* was found at six of the sites in 1915, but only three in 1992. *Hyla regilla*, in contrast, was only lost from one of the eight sites where it was present in 1915. Merced Lake was the only site where heavy stocking began before the Grinnell and Storer survey. At this site *H. regilla* was the only species found in either survey.

Widespread introduction of fish has evidently limited the distribution and overall numbers of some frog species, particularly *R. muscosa*. It does not adequately explain the overall decline of the frog fauna in the Yosemite area, however, for several reasons. First, most or all of the frog species in the area are apparently capable of surviving and reproducing in waters containing fish, as long as there is emergent vegetation or other escape cover (Cory 1963; Fellers & Drost 1993; present study). *R. muscosa* seems to be most susceptible to fish predation, yet it remained the most numerous frog species in Westfall Meadows as late as 1977, long after fish were introduced (Yoon 1977). It has since disappeared from that area. Also, the toads are much less susceptible to adverse effects of introduced fish for two reasons: 1) toads frequently breed in ephemeral bodies of water thar do not harbor fish; and 2) the true toads produce toxic skin secretions, so fish tend to avoid them (Peterson & Blaustein 1991).

In addition, frog populations have disappeared from sites that either were never planted with fish or that are too small or ephemeral to support fish. For example, Tuolumne Meadows and the Tioga Pass area contain extensive meadow pools and marshes that are effectively isolated from fish. *Rana muscosa* has disappeared from these areas entirely, whereas *B. canorus* has disappeared from Tuolumne Meadows and dwindled to a remnant population at Tioga Pass (Kagarise Sherman & Morton 1993). Finally, what is known of the timing of the population declines does not agree with introduced fish being the sole or primary cause. Large numbers of trout were planted in Yosemite National Park waters between 1932 and 1951, with peaks of over 1,000,000 fish per year in the late 1930s and 1940s. Since 1951, the number of fish planted has steadily declined (Elliot & Loughlin 1995). Significant declines of *B. canorus*, *R. muscosa*, and other species have occurred later than this.

DROUGHT

Between 1987 and 1992 California experienced a severe and unusually long drought (Roos 1992; Fig. 3), which undoubtedly had adverse effects on some frog popula-

Table 4. Stocking records of trout in some lakes and streams of Yosemite National Park[a] and changes in amphibian populations at those sites between 1915[b] and 1992[c].

		Amphibians	
Area	*Stocking date*[d]	*1915*	*1992*
Indian Creek	1935–1937	*Bufo canorus*	
		Hyla regilla	*Hyla regilla*
		Rana muscosa	
Lyell Fork	1925–1963[e]	*Bufo canorus*	*Bufo canorus*
		Rana muscosa	
McGee Lake	1936–1951	*Hyla regilla*	*Hyla regilla*
		Rana muscosa	
Merced Lake	1892–1948	*Hyla regilla*	*Hyla regilla*
Porcupine Creek	1927–1948[e]	*Bufo canorus*	*Bufo canorus*
		Hyla regilla	*Hyla regilla*
		Rana muscosa	
Tamarack Creek	1927–1952[e]	*Bufo canorus*	
		Hyla regilla	
Tuolumne Meadows	1931–1961[e]	*Hyla regilla*	*Hyla regilla*
		Rana muscosa	
Vogelsang Lake	1930–1968	*Bufo canorus*	
		Hyla regilla	*Hyla regilla*
		Rana muscosa	
Young Lakes	1935/1949	*Bufo canorus*	*Bufo canorus*
		Hyla regilla	*Hyla regilla*
		Rana muscosa	

[a] *Elliot & Loughlin 1995.*
[b] *Grinnell & Storer 1924.*
[c] *This study.*
[d] *Stocking date indicates the first known large-scale stocking effort that resulted in a persistent fish population (as determined by later surveys for fish).*
[e] *Some earlier small-scale stocking.*

tions in the area. Some mapped ponds visited during the 1992 survey had dried up entirely, and some meadow areas were very dry. Such dry conditions have the most severe effect on amphibians closely associated with water throughout their life cycle and those that have multiyear aquatic larval stages, such as *R. muscosa*. We believe, however, that the drought has mainly had an exacerbating or compounding effect on the observed declines, rather than being a primary cause. Even a severe drought should not lead to widespread disappearance of species in an area such as California, where prolonged droughts are a regular occurrence. The Grinnell and Storer survey also took place during a lengthy dry period (particularly the latter part of the survey; Fig. 3), so comparisons between our surveys should not be significantly biased in this regard. Yoon (1977) reported that *R. muscosa* was still common in Westfall Meadow in 1977, at the end of a drought that was shorter than the present one, but had much lower annual rainfall totals (Fig. 3). As noted, this species disappeared from Westfall Meadow sometime since 1977. Finally, declines of *B. canorus, R. aurora, R. boylii,* and *R. muscosa* have been occurring over 20–30 years (Bradford et al. 1994; Kagarise Sherman & Morton 1993; Moyle 1973). Except for the current drought, most of this period has been wetter than normal.

COMPOUNDED FACTORS

Some recent studies have evaluated possible combinations of factors (generally natural forces compounded by anthropogenic influences) as explanations for amphibian declines and losses (Carey 1993; Pounds & Crump

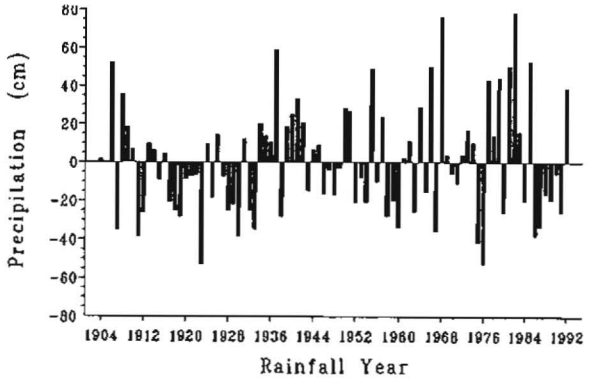

Figure 3. Wet and dry periods in the Yosemite area of the California Sierra Nevada, as indicated by departure of annual precipitation totals from the mean (mean = 90.1 cm) over the period 1904–1993. Negative values indicate lower than mean, and positive values indicate greater than mean precipitation.

1994). In a study of *R. muscosa* in the southern Sierra Nevada, Bradford et al. (1993) hypothesized that introduced fish in streams and other permanent waters may effectively restrict frog populations to isolated areas of fish-free habitat. Loss of such small, isolated amphibian populations has been documented in a number of areas (Bradford 1991; Corn & Fogleman 1984; Sjögren 1991), and the presence of fish in intervening streams and ponds may prevent dispersing frogs from moving back to recolonize such sites when a local population disappears.

The hypothesis presented by Bradford et al. (1993) reflects a metapopulation model of persistence for *R. muscosa*. Such a metapopulation structure may exist for many amphibian populations because of their use of discrete aquatic breeding sites, isolated to varying degrees from other such sites. However, *R. muscosa* populations prior to the introduction of fish probably corresponded more closely to "mainland-island" metapopulations rather than to classical metapopulations (cf. Harrison 1991). The large lake populations present at the time of the Grinnell and Storer survey, numbering into the thousands of individuals, probably served as major sources of emigrants to smaller or less suitable habitats. These large lake populations were no longer present by the 1992 survey, and remnant frog populations were small and isolated. Remaining fish-free habitats—small marshes, overflow ponds, and glacial potholes—are more prone to drying during drought periods. Hence, peripheral populations of *R. muscosa*, isolated since the widespread introduction of fish into permanent waters, may have been experiencing gradual attrition during periods of severe drought, as occurred between 1987 and 1992.

Conclusions

The hypothesis presented above may account for the present status of *R. muscosa* in the Sierra Nevada, but does not seem to explain the losses documented among other amphibian species. The toads, in particular, are less affected by fish predation; we noted several sites where *B. boreas* or *B. canorus* adults and tadpoles were present in waters with fish. Also, the low-elevation frogs and toads evolved with native fish and have been exposed to non-native fish for longer periods of time. Hence, we cannot account for the broad scale of the observed declines across species and across a large geographic area. Serious questions remain about the cause or causes of the declines in the Yosemite area, the extent to which the declines are related, and the relationship between these losses and those reported in other areas of the world.

Other studies have demonstrated similar declines, losses of local populations, and probable extinctions of anuran species in areas of relatively undisturbed habitat (Bradford et al. 1994; Carey 1993; Fellers & Drost 1993; Pounds & Crump 1994). We echo concerns voiced by others regarding declines of amphibians in different areas of the world. There continues to be a dearth of information to define the extent and seriousness of the problem on a large scale; hypotheses have been presented in some cases, but there remains a frustrating lack of clear answers for many declines.

Acknowledgments

The Yosemite Association provided funding for this study. Yosemite National Park Research Scientist Jan van Wagtendonk encouraged the project from its inception, and provided help with planning and logistics. David Wake and Jens Vindum provided access to original field notes as well as data on amphibians in collections. Yosemite National Park personnel Maureen Loughlin, Steve Thompson, and Martha Elliot assisted with background ecological information, particularly on fish stocking within the Park. Stephen Veirs provided administrative support and helpful discussion. Brian Yost supplied stream gaging data and rainfall data for stations within Yosemite National Park. Craig Fellers, Scott Fellers, and Rebecca Hamman assisted with fieldwork in 1992; Jenny Ellingson and Bridget Keimel assisted with follow-up surveys in 1993.

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