Herpetological Conservation and Biology 2(1):5-21
Submitted: 21 September 2006; Accepted: 10 January 2007

DEMISE OF REPATRIATED POPULATIONS OF MOUNTAIN YELLOW-LEGGED FROGS (*RANA MUSCOSA*) IN THE SIERRA NEVADA OF CALIFORNIA

GARY M. FELLERS[1], DAVID F. BRADFORD[2], DAVID PRATT[1] AND LESLIE LONG WOOD[1]

[1]U.S. Geological Survey, Western Ecological Research Center, Point Reyes National Seashore, Point Reyes, CA 94956, USA, e-mail: gary_fellers@usgs.gov
[2]U.S. Environmental Protection Agency, Landscape Ecology Branch, P.O. Box 93478, Las Vegas, NV 89193, USA

***Abstract.*—In the late 1970s, *Rana muscosa* was common in the Tableland area of Sequoia National Park, CA. Surveys in 1993-1995 demonstrated that this frog had disappeared from this and other areas, even though the species was still common 30 km to the northeast. To evaluate potential causes of the extirpation, we repatriated *R. muscosa* eggs, tadpoles, subadults, and adults to four previously occupied sites in the Tableland area in 1994 and 1995. We surveyed the release sites every few days in the summers of 1994 and 1995, and once a month in 1996-1997. During the first week after release, survival of all life history stages was high at each of the release sites. At the end of the first summer there were metamorphosing tadpoles, and adult frogs were still present. However, we detected no evidence of reproduction at three sites and nearly all life history stages disappeared within 12 months. At the fourth site, there was limited reproduction, but it was not sufficient to maintain a population. It appears either that the causal factors for the demise of *R. muscosa* in the 1970s were still operating in the 1990s, or that a new limiting factor has developed. Dispersal, weather, water quality, and predation do not appear to be causative agents; because fish have never been present in the portions of the watershed where we were working, they were not a factor. Observations and data are consistent with the hypotheses that chytridiomycosis, caused by the chytrid fungus *Batrachochytrium dendrobatidis*, and/or exposure to airborne pesticides caused both declines. However, at the time of our study, chytridiomycosis had not been described and the potentially significant role of contaminants was largely undocumented.**

Key Words.—amphibian; chytridiomycosis; *Rana muscosa*; park management; pesticides; population decline; repatriation

INTRODUCTION

Rana muscosa (Fig. 1) was once abundant throughout much of the Sierra Nevada (Grinnell and Storer 1924) and was common as recently as the 1970s (Bradford et al. 1994a). By the mid-1990s, however, *R. muscosa* had suffered conspicuous declines in the southern Sierra Nevada. Surveys of 670 sites in Sequoia and Kings Canyon National Parks in 1993-1995 indicated that *R. muscosa* was apparently extirpated from more than half of suitable locations (Gary Fellers, unpubl. data), including the study sites where Bradford found the species to be abundant in the late 1970s. However, *R. muscosa* was still common in some areas at the time of our work (e.g., Sixty Lakes Basin, Kings Canyon National Park).

FIGURE 1. The Yellow-legged Frog, *Rana Muscosa*. Photographed by Gary M. Fellers.

Dodd and Siegel (1991) and Dodd (2005) point out that programs to reestablish amphibian populations are often flawed by not investigating the causes for the original decline or extirpation. We designed our study to address this concern. Specifically, we wanted to evaluate the factors that might contribute to the decline of *R. muscosa*. Our goal was not to reestablish a viable population of *R. muscosa*. We expected that whatever caused the original loss would still be present, and that the repatriated frogs would likely decline. We conducted this study to recreate the conditions surrounding the loss of *R. muscosa* so we could evaluate causes of decline. We gathered data on growth, survival, dispersal, weather, water quality, predation, and contaminants along with data on survival of all life history stages, and reproductive effort (e.g. presence of new egg masses). Unlike most areas within the range of *R. muscosa* in the Sierra Nevada, the repatriation site never had fish in the upper portions of the watershed where our study took place, so fish were not a factor. Unfortunately, our study was carried out several years prior to the description of chytridiomycosis in amphibians (Berger et al. 1998), and before pesticide drift from the Central Valley of California had been recognized as a potentially significant problem for Sierra Nevada amphibians (Sparling et al. 2001), so we never examined

TABLE 1. *Rana muscosa* repatriated from Sixty Lake Basin (Kings Canyon National Park) to Tableland sites (Sequoia National Park, California).

		14 – 16 June 1994			20 September 1994	26 August 1995		
Release Site	Egg Masses	2nd year Tadpoles	3rd year Tadpoles	Subadults	Adults	2nd year Tadpoles	3rd year Tadpoles	Adults
Table Meadow	2	80	84	25	0	0	0	0
Frog Lake	2	80	84	24	0	96	108	31
Far Pond	2	80	84	25	25	94	108	31
Full Moon Pond	2	78	84	23	25	96	108	31
Totals =	8	318	336	97	50	286	324	93

frogs or tadpoles for chytridiomycosis and only looked at pesticides as the repatriated frogs were dying off (Fellers et al. 2004).

METHODS

Study Animal.—*Rana muscosa* breeds in high mountain ponds, lakes, and some streams in the Sierra Nevada at elevations from approximately 1500-3700 m (Zweifel 1955). Eggs are laid immediately after snowmelt and tadpoles typically do not metamorphose until their third summer (Vredenburg et al. 2005). During mid-summer, nominal tadpole age classes are readily distinguished. First-year tadpoles are relatively small (< 40 mm total length), second-year tadpoles are appreciably larger with minute hind limbs (Gosner stage < 36; Gosner 1960), and third-year tadpoles have conspicuous hind limbs (Gosner stage ≥ 36). At our study areas, male *R. muscosa* develop secondary sexual characteristics when they reach approximately 4.5 cm snout-vent length, and weigh about 10 g. We refer to frogs > 4.5 cm as adults, and frogs less than that size as subadults.

Study Area.—We selected the Tableland area of Sequoia National Park (Fig. 2; 36°37'05"N, 118°38'16"W) because of (1) the absence of *R. muscosa* in 1993; (2) the existence of large populations of *R. muscosa* within the previous 20 years; (3) availability of historic data on population size; (4) lack of non-native predators (e.g., trout); and (5) isolation from extant populations of *R. muscosa* that could disperse to our study area. During the 1970s, the Tableland area supported many hundreds of adult and larval *R. muscosa* within a 15 km^2 area (Bradford 1991; Bradford et al. 1994a). Population declines were first noted in the late 1970s and the last *R. muscosa* was seen in the Tableland area in 1989 when a few tadpoles were found (Bradford et al. 1994b); none were found at the same site in 1991. In 1993, Bradford and Fellers spent a week surveying all suitable frog habitat within the Tableland and found no *R. muscosa*, either in that watershed or in the upper reaches of the adjacent watersheds. Since it is relatively easy to detect adults and tadpoles in the clear, nearly vegetation-free ponds and lakes of the high Sierra, it is unlikely that we overlooked extant populations during repeated surveys prior to the experimental repatriation.

FIGURE 2. Far Pond is located in the Tableland area of Sequoia National Park. Photographed by Gary M. Fellers

Unlike many places in the Sierra Nevada, the Tableland area lacked fish; hence, they could not have played a role in the decline or in our experimental repatriation. Migration of *R. muscosa* to and from the Tableland area during our study was unlikely. Non-native, predaceous trout inhabited all the streams in surrounding watersheds and at lower elevations in the Tableland watershed. Thus the streams could not easily serve as recolonization or dispersal corridors for *R. muscosa*. The nearest known *R. muscosa* population was more than 10 km away, much greater than the 1 km that *R. muscosa* occasionally move (Vredenburg et al. 2005).

Rana muscosa were released at four sites (Fig. 3). Table Meadow is a 4.5 ha meadow (3,110 m elevation) with a stream running through it. Frog Lake is a small lake (2 ha, 4.1 m maximum depth, 3,080 m) that lies 250 m southwest of Table Meadow. In the late 1970s, it supported a large population of *R. muscosa*. Far Pond (1 ha, 2.7 m maximum depth, 3,290 m) is one of a chain of ponds at the head of a small drainage. Full Moon Pond (1 ha, 2.6 m maximum depth, 3,230 m) is also at the head of a small drainage. *Rana muscosa* populations existed at all four of these sites in the late 1970s. Frog Lake and Far Pond were referred to as sites G-013 and G-049 by Fellers et al. (2004). The third pond downstream from Far Pond was referred to as G-054 by these authors, whereas we have designated it Dispersal Pond 3 (Fig. 4).

Criteria for selecting the donor area were: (1) a large population of apparently healthy *R. muscosa*; (2) elevation within 150 m (500 ft) of the release sites; (3) proximity to the Tableland area; and (4) a genetically

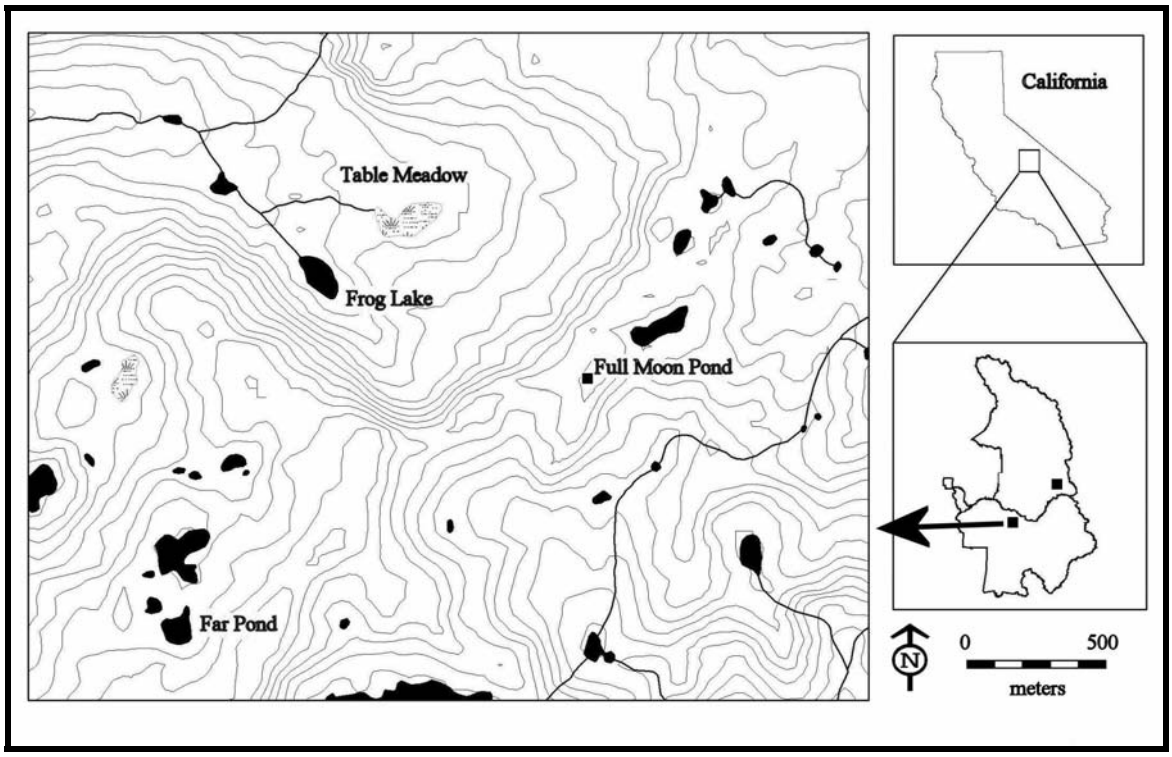


FIGURE 3. Location of the four *Rana muscosa* release sites in the Tableland area of Sequoia National Park, California. Map based on USGS 1:24000 Lodgepole, California topographic map. Inset shows outline of Sequoia and Kings Canyon National Parks with the northeastern square showing the location of Sixty Lakes Basin.

diverse group of donor populations. Sixty Lake Basin in Kings Canyon National Park (36°48'35"N; 118°25'29"W) was selected as the donor area. The basin was one of the closest areas to the release sites (30 km) that still supported substantial populations of *R. muscosa.* During our 1993-1994 surveys, we found 1,718 adult frogs, 1,289 subadults, and 16,027

larvae at 65 sites within the basin. We limited the impact on donor populations by collecting only from the largest populations, and by not removing more than 20% of any life history stage, i.e., egg, tadpole, subadult, or adult. Usually, we removed < 5% of any one stage. The donor site elevations (3,250-3,345 m) were similar to that of the Tableland release sites. The area had also been identified as having one of the most genetically diverse populations of *R. muscosa* in the southern Sierra Nevada, based on mitochondrial DNA analysis (Bradley Shaffer and Gary Fellers, unpubl. data).

Repatriations.—On 11-14 June 1994, eight egg masses, 468 second-year tadpoles, 624 third-year tadpoles, and 97 subadult frogs were collected from nine ponds at Sixty Lake Basin (Table 1). The number of tadpoles subsequently released was almost 40% lower due to mortality during the 1-3 day holding period. We did not segregate frogs and tadpoles based on where they were collected. Subadult frogs were placed in plastic boxes with six, 5.0 mm holes drilled in the lids to allow air circulation. The frogs were kept moist with wet paper towels, which were changed once or twice a day. Eggs and tadpoles were held in 4.0 l plastic freezer bags that were left open at the top. Tadpole densities were approximately 25 per bag. Each egg mass was placed in its own bag. Water was changed every 1-2 hours throughout the day and 3-4 times during the night. On 14 June, the Ziploc bags were closed and all life stages were flown to the release sites by helicopter.

On 15-16 September 1994, 50 adult frogs (25 male, 25 female) were collected from five ponds at Sixty Lake Basin (Table 1). They were held as described above for subadults. On 16 September, the frogs were backpacked 18 km to the nearest trailhead, where each frog was anesthetized with benzocaine, measured (snout-vent length), weighed (to nearest 0.1 g), and marked with a PIT tag (Fellers and Freel 1995). The frogs were then backpacked 13 km into the Tableland where they were released on 20 September.

On 24 and 25 August 1995, 93 adult frogs (46 males and 47 females), 286 second-year tadpoles, and 324 third-year tadpoles were collected at Sixty Lake Basin (Table 1). The adult frogs were anaesthetized, weighed, measured, PIT-tagged, and held using the same techniques as in 1994. Unlike 1994, tadpoles were collected and put into fiberglass screen cages set in the water at the edge of a

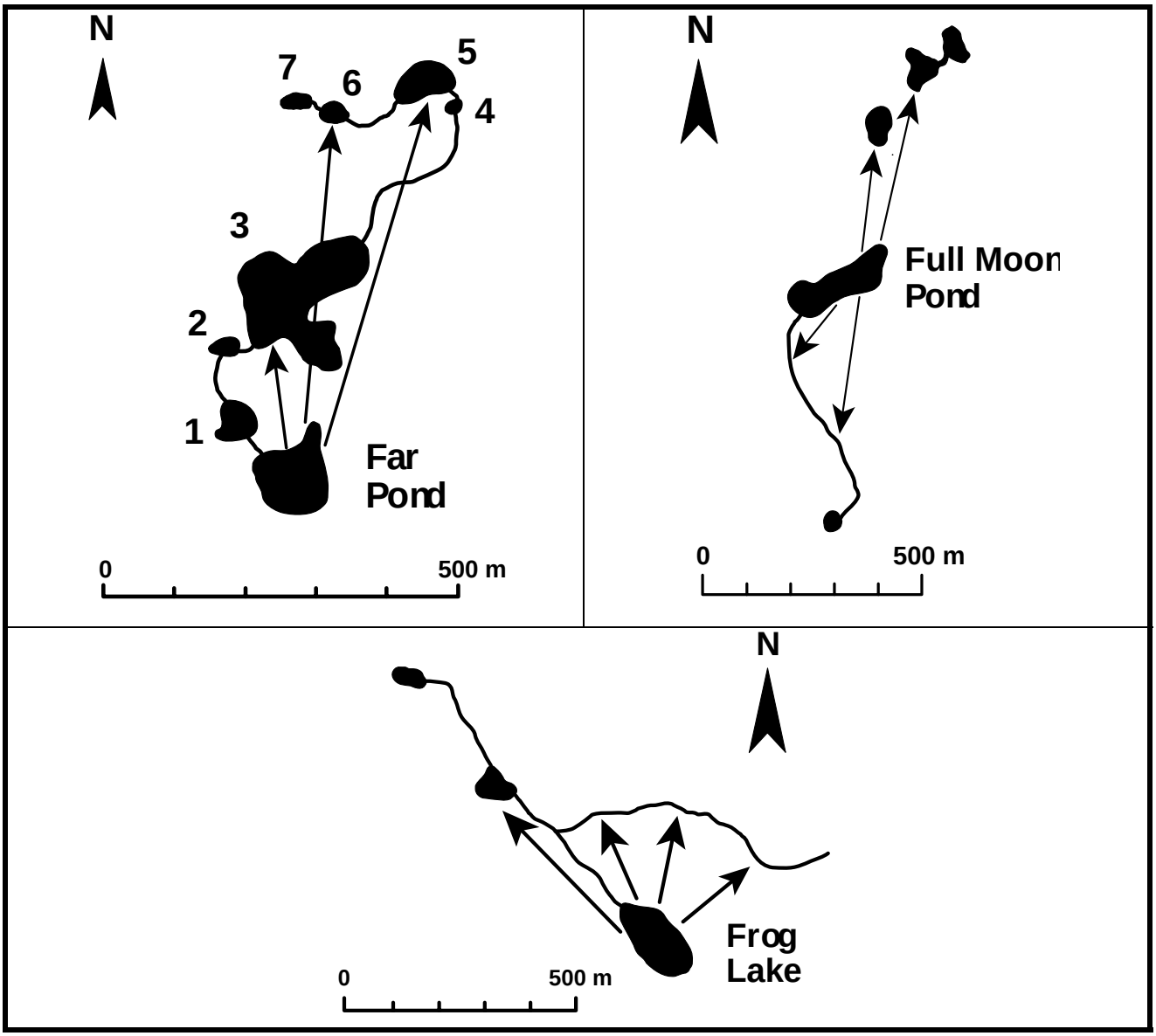


FIGURE 4. Dispersal of *Rana muscosa* from repatriation sites, Sequoia National Park. Adjacent ponds (numbered for Far Pond) are referred to as dispersal Ponds. Arrows in the figures indicate the sites where dispersing frogs were last detected. For Far Pond, 12 frogs dispersed to Dispersal Pond 3, one frog to Dispersal Pond 5, and one frog to Dispersal Pond 6. See Fig. 3 for location map.

pond. On 26 August, they were transferred to 4.0 l Ziploc bags for about 45 min during transport to the Tableland by helicopter.

At the release sites, about 10% of the water was poured out of the container every 5-10 min, and a similar amount of fresh pond water was added back in so that eggs and tadpoles could adjust to differences in water temperature and chemistry. In 1994, amphibians at Table Meadow, Frog Lake, and Full Moon Pond were released after an hour into a 2 x 1.5 x 1 m (L x W x H) temporary holding cage made of fiberglass screen supported by PVC pipe. The release cage was set at the edge of the pond so that one end was almost submerged and the other end was resting on the shore. This provided conditions suitable for both aquatic and terrestrial life history stages. Lettuce was added to each cage as a food supplement. Tadpoles were released after two days. At Far Pond, the pond was still 80% frozen during the day, and darkness and refreezing of the pond at dusk prevented use of a holding cage. It was necessary to break the ice and release the eggs, tadpoles and subadult frogs directly into the pond after one hour of acclimation. In 1995, second-year and third-year tadpoles, and adult frogs were released at three of the four Tableland sites after being held in fiberglass screen cages for a few hours. (For details of the repatriation methods see: Fellers, G.M., D.F. Bradford, D. Pratt, and L. Wood. In press.

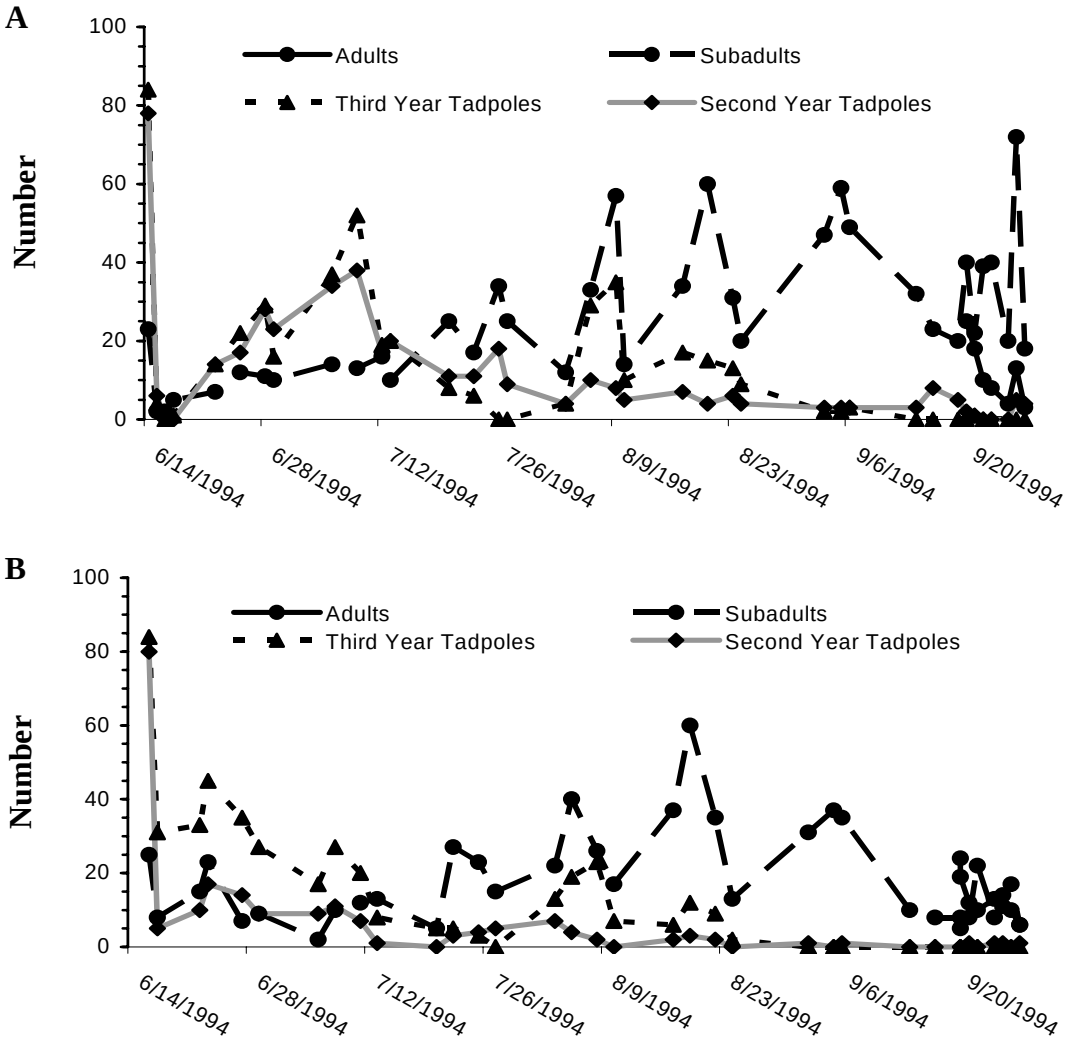


FIGURE 5. Counts of *Rana muscosa* at Far Pond (A) and Full Moon Pond (B) and the adjacent dispersal ponds, Sequoia National Park, in 1994. Egg masses, second-year tadpoles, third-year tadpoles, and subadult frogs were released on 14 June 1994. Adult *R. muscosa* were released 20 September 1994. On those days, the number graphed represents the actual number released. See Table 1 for numbers of each life history stage repatriated.

Experimental translocation of mountain yellow-legged frogs (*Rana muscosa*) in the Sierra Nevada of California. USGS Technical Publication).

In 1994, we conducted diurnal visual surveys for amphibians at each release site every 1-3 days from the initial release until the onset of heavy snowfall on 27 September. In 1995, monitoring extended from the time that ice melted (1 August) until 20 October, when ice was forming nightly on the higher elevation ponds. The sites were also monitored at approximately monthly intervals during the summers of 1996 and 1997, and during a single visit in September 1998.

Monitoring consisted of counting all life history stages of amphibians using visual encounter surveys (Crump and Scott 1994; Fellers and Freel 1995). When adult frogs were released at the Tableland sites (20 September 1994), monitoring was extended to include connecting streams and ponds within several hundred meters of all four release sites to evaluate dispersal. In 1995, adult frogs were caught at two-week intervals, scanned for PIT tags, weighed, measured, and examined for signs of disease or injuries. Frogs were also captured and examined in a similar fashion during surveys in 1996-1998.

During 1994 and 1995, we carefully surveyed each site for predators once each week. Western Terrestrial Garter Snakes (*Thamnophis elegans*) were captured when possible and palpated to determine if they had a food bolus. Snakes with a bolus were encouraged to regurgitate it (Filippi et al. 2005) for identification of food items.

Environmental Measurements.—At one-week intervals throughout the summers of 1994 and 1995, we measured pH and electrical conductivity (EC) at the release sites. Water samples were analyzed at our Tableland base camp after calibration of the equipment (pH meter, Accumet, model 1001; Fisher Scientific, Los Angeles, California,

TABLE 2. Counts of *Rana muscosa* at Far Pond and adjacent dispersal ponds in 1996-1998.

Date	Tadpoles		Subadults	Adults		
	2nd Year	3rd Year		Repatriated[1]	Recruits[2]	Not Captured
7/10/96	0	0	2	2	3	3
7/12/96	0	0	5	9	2 + 1 dead	9
8/22/96	1	28	16 + 2 DEAD	6	23	1
10/1/96	0	0	6	7	7	1
10/3/96	0	0	10	10	11	1
7/15/97	0	0	0	2	9 + 2 dead	1
7/16/97	0	1	1	1	3 + 2 dead	5
7/17/97	0	2	0	1	5 + 1 dead	2
7/20/97	0	4	1	1	10	1
8/19/97	0	0	5	4	11 + 1 dead	0
9/19/98	1	0	0	0	1	0

1. Repatriated frogs were captured at Sixty Lake Basin, PIT-tagged, and released at Far Pond in 1994 or 1995.
2. Recruits were adults without PIT tags when first captured at Far Pond in 1996-1998. Hence, they developed into adults at Far Pond from tadpoles or subadults that had been repatriated in 1994 or 1995.

USA; electrical conductivity meter, Hach Mini Conductivity Meter, model 17250; Hatch, Loveland, Colorado, USA).

On 5 August 1994, two temperature loggers (StowAway; Onset, Pocasset, Massachusetts, USA) were deployed in Far Pond at depths of 0.5 and 1.0 meters above the bottom, at a time when the water level was slightly more than a meter deep. The data loggers were retrieved on 23 August 1995; the data loggers remained at 0.5 and 1.0 m above the bottom, but the water level in the pond had increased by about one meter. Water temperature was monitored at Full Moon Pond, Frog Lake, and Far Pond from 26 September 1995 to 21 August 1996. At each pond, one logger was weighted and placed on the bottom of the pond at the deepest point; the other logger floated on the surface. Long-term weather data (temperature, precipitation) were obtained for the National Weather Service weather station at Grant Grove, California, USA (36°44'21"N, 118°57'51"W), 32 km NW of the Tableland at an elevation of 1990 m (6,530'). Data have been collected since 1 November 1940 and were obtained from the National Climatic Data Center (www.ncdc.noaa.gov).

On 18-20 August 1997, we were able to find only 20 *R. muscosa* in the Tableland area. All 20 frogs were collected, including 12 adult males, three adult females, and five subadults. Sixteen of the frogs were collected at Far Pond. Two frogs were collected at Dispersal Pond 3 (Fig. 4), and one was collected at Frog Lake. Each frog was anaesthetized, weighed, measured, and frozen in liquid nitrogen. On 22 August 1997, 20 *R. muscosa* from Sixty Lake Basin donor sites were collected (10 adult males, 5 adult females, and 5 subadults) and similarly processed. All frogs from both the Tableland and Sixty Lake Basin were analyzed for pesticide concentrations in their tissue (see Fellers et al. 2004 for methods). At two ponds in the Tableland and two in Sixty Lake Basin, concurrent 4-liter water samples were also collected. Water was filtered through a glass fiber filter and extracted using a 4-g C18 solid-phase extraction cartridge [see LeNoir et al. (1999) for detailed description of the sample collection, processing, and analysis methods].

Data were analyzed using Statistix (version 8.0, Analytical Software, Tallahassee, Florida, USA). Mann-Whitney and Wilcoxon paired sample non-parametric tests were used because our data were not normally distributed. We used $\alpha = 0.05$ to evaluate statistical significance. Measures of variability are given as standard deviations.

RESULTS

Short-term Survival.—Eight egg masses, 1264 tadpoles, 97 subadults, and 143 adult frogs were released at the Tableland (Table 1). We evaluated their survival during the first week after repatriation. During that time, all egg masses drifted from their original positions. We lost track of two of the eight egg masses after one day, and could not find any egg masses after five days, hence we could not evaluate whether the eggs hatched. Though there was significant mortality of tadpoles while holding them prior to transport in 1994, survival during transport and release was > 99% in both 1994 and 1995. No subadult frog mortality occurred during collecting, holding, or transport. Three subadults died during the release at Far Pond, largely because the release was carried out in the dark when the pond surface was refreezing. We incurred no mortality among the adult frogs repatriated from Sixty Lake Basin to the Tableland in either 1994 or 1995.

Long-Term Survival of Tadpoles and Subadults.—In 1994, we conducted more than 30 surveys at each of the four Tableland sites (Fig. 5–6). Several patterns were evident: (1) Counts for all life stages varied considerably among surveys, even for surveys within a few days of each other. Some, but not all, of the low counts were on days with cold, windy, or rainy weather; (2) the number of subadults in late summer exceeded the number released in June, demonstrating that some tadpoles successfully metamorphosed; (3) the number of tadpoles counted during early summer was usually well below the number actually present as shown by the number of recently metamorphosed subadults observed at the end of the season. Only a fraction of the repatriated tadpoles were

TABLE 3. Concentration of pesticides (ng/g wet wt) in *Rana muscosa* tissue collected at the Tableland (Sequoia National Park, n = 20), and the Sixty Lakes Basin (Kings Canyon National Park, n = 20) California, USA, 18-22 August 1997 (from Fellers et al. 2004).

	α-HCH[a]	γ-HCH[a]	γ-chlordane	trans-nonachlor	α-endosulfan	*p,p'*-DDE[b]
Tableland	1.16	0.07	0.71	1.72	0.50	46.72
Median	1.41	103.1	0.84	2.66	0.56	45.69
Mean	1.24	221	0.75	2.60	0.36	19.92
Standard Deviation						
Sixty Lakes	1.12	0.15	0.14	0.46	0.41	19.34
Median	3.95	0.37	0.17	0.53	0.45	16.96
Mean	4.56	0.48	0.24	0.59	0.24	7.88
Standard Deviation	0.29	0.71	0.00	0.00	0.31	0.00

a. HCH = hexachlorocyclohexane,
b. DDE = dichlorodiphenyldichloroethylene,
c. Mann-Whitney *p*-value using Chi-squared approximation

observed at any one time, even within a few days of release; (4) because tadpole counts were so low, it is not possible to determine if second-year tadpoles survived to their third summer; and (5) counts for both second- and third-year tadpoles declined to or near zero by late summer.

In 1995, we conducted nine surveys at Table Meadow between 1 August and 17 October, but no frogs, tadpoles, or eggs were found. We conducted 17-20 surveys at the three sites where tadpoles and adult frogs were released in August 1995 (Fig. 7). As in 1994, the survey counts were highly variable. Counts of subadults (which were released only in 1994) were substantially lower in 1995 than in 1994 at both Full Moon Pond (1994: median = 15, n = 32 counts versus 1995: median = 1.5, n = 20) and Frog Lake (1994: median = 10, n = 32 versus 1995: median = 0, n = 17), but were similar between years at Far Pond (1994: median = 34.5, n = 20 counts versus 1995: median = 22, n = 37). The absence of subadults at Full Moon Pond and Frog Lake during the early part of the 1995 season, and low numbers of subadults later in the season, suggest that subadults did not survive from 1994 to 1995. In contrast, many of the subadults at Far Pond survived the winter of 1994-1995. Tadpole counts were zero or near zero at all three sites at the beginning of the 1995 season, consistent with counts at the end of the 1994 season. First-year tadpoles were observed at only Far Pond. Three were found on 3 October, and four on 10 October. These tadpoles came from eggs oviposited at Far Pond in 1995.

During 1996-1998, *R. muscosa* tadpoles were found at all three Tableland pond sites. Nearly all of these were third-year tadpoles. The maximum counts in 1996 were substantially greater than counts at the end of 1995 (Fig. 5). The increase in tadpoles may have occurred in 1995 as well, but it would have been masked by the repatriation of additional tadpoles in 1995.

No subadults were found at Full Moon Pond or Frog Lake in July 1996, suggesting that none survived from 1995 (Fig. 7). At Far Pond, the low subadult numbers in July 1996 (compared to the number counted at the end of 1995) suggest that mortality was also high during the winter of 1995-1996 (Table 2, Fig. 5A). Subsequent declines of second-year tadpoles, third-year tadpoles, and subadults at Far Pond during 1996-1998 indicate a loss due to metamorphosis and/or mortality, and little recruitment. The only documentation of reproduction during 1996-1998 was a single second-year tadpole found in Dispersal Pond 3 (Fig. 4) in 1998, three years after the last second-year tadpole had been released.

Survival and Recruitment of Adults.—In 1994, adult frog numbers at both Far Pond and Full Moon Pond rapidly declined to approximately 2/3 of the number released (Fig. 5). By 1995, frog counts at those two ponds differed from each other greatly (Fig. 7). At Full Moon Pond, none of the 25 frogs repatriated in 1994 was ever seen after 1994. At Far Pond, 15 of the 25 frogs released in 1994 were captured in 1995, seven of the original 25 in 1996, and three in 1997. In 1995, all 31 of the adults released that year at Far Pond were captured at least once during the summer; 15 were captured again in 1996, and two in 1997. At the other two sites, fewer frogs were captured in 1995 than at Far Pond, and only two frogs were found after 1995, both at Full Moon Pond at the start of 1996.

After 1995, we found only three of the repatriated adult frogs, one at Frog Lake, and two at Full Moon Pond. Recruitment of adults from eggs, tadpoles, or subadults occurred only at Far Pond (Table 2), as shown by the presence of adult frogs lacking PIT tags. In contrast, untagged adult *R. muscosa* were found at Far Pond in both 1996 and 1997. We tagged a total of 28 frogs there, 14 adults and 4 subadults in 1996, and 10 adults in 1997. Some of the adult frogs found at Far Pond in 1996 and in 1997 were not captured (Table 2). Because none of the unmarked adults was found until 1996, it seems likely that they developed from tadpoles released at Far Pond, rather than from the 25 (untagged) subadults released there in June 1994. On 15-17 July 1997, all the frogs we found either appeared sick or were dead; two were found dead and three died within a day of capture (Table 2). On 19 August 1997, all 20 frogs observed at our repatriation sites

(19 at or near Far Pond, one at Frog Lake) were collected for analysis of pesticides. Only one frog was observed during the 1998 survey. However, four adult frogs were found Dispersal Pond 3, downstream from Far Pond (Fig. 4) in 2000, and one was found there in 2001 (Roland Knapp, pers. comm.).

Dispersal from Release Site.— Far Pond was the site with the most suitable frog habitat in the immediate vicinity and we detected significantly more dispersal at Far Pond where 14 of the 56 released frogs (25%) were later found in nearby ponds, compared to 8 of 79 repatriated frogs (10%) at the other three sites combined ($\chi^2 = 6.54$, $P = 0.0106$). No appreciable difference was found in the dispersal frequency of males and females; of the 22 dispersing frogs, 12 were females and 10 were males. Maximum straight-line dispersal distance ranged from 50 m to 510 m, with a median of 80 m (mean = 173 ± 138 SD).

Some frogs were detected at increasingly greater distances from their release site. Frog 7112 was released at Far Pond on 20 September 1994; it was found in Dispersal Pond 1 (25 m from Far Pond) on 21 September 1995, and was found in Dispersal Pond 3 (90 m from Far Pond) on 3 October 1996 (Fig. 4). Frog 6744 was released on 20 September 1994; it was found in Dispersal Pond 5 on 5 September 1995 and 10 October 1995, and in Dispersal Pond 6 on 19 October 1995 (Fig. 4). The total distance from Far Pond to Dispersal Pond 6 (via the connecting stream) was $\geq$ 800 m.

TABLE 4. Concentration of pesticides (ng/liter) in surface water samples collected at the Tableland (Sequoia National Park) and the Sixty Lakes Basin (Kings Canyon National Park), California, 18-22 August 1997 (from Fellers et al. 2004). Log K_{ow} is an indicator of the degree to which a substance will bioaccumulate. Far Pond is referred to as G-049 in the table below.

			Tableland		Sixty Lakes	
Compound	Log K_{ow}	Limit of Detection[a]	G-049	G-054	S-545	S-471
γ-chlordane	5.2[b]	0.03			0.27	
α-chlordane	5.2[b]	0.03				
Chlorpyrifos	4.3[b]	0.03	12	0.72	0.22	0.17
pp-DDE	6.9[c]	0.1			0.31	
o,p'-DDT	6.8[b]	0.1			0.46	
p,p'-DDT	6.9[c]	0.1				
Diazinon	3.4[b]	0.06	3.1	3.4	1.8	
α-endosulfan	3.6[d]	0.03	0.78	1.0	0.30	0.37
β-endosulfan	3.6[d]	0.05	0.40	0.42	1.8	0.17
endosulfan sulfate		0.03	2.9	2.2	0.33	0.40
α-HCH	3.81[d]	0.03				0.29
γ-HCH	3.8[d]	0.03				
trans-nonachlor		0.04			0.31	
Trifluralin	4.6[b]	0.1			2.5	

a. Analytical detection limit was three times the standard deviation of blank levels (LeNoir et al. 1999).
b. Selected values from Finizio et al. 1997.
c. de Bruijn et al. 1989.
d. Selected values from Suntio et al. 1988.

Frog 7026 dispersed away from the release sites and then returned. On 26 August 1995, frog 7026 was released at Frog Lake; on 21 September 1995, it was > 200 m away in the stream flowing through Table Meadow; on 5 October 1995, it was back in Frog Lake.

Not all dispersal was closely associated with water; in a few cases, the dispersal was across land. The route from Full Moon Pond to the two ponds to the north (Fig. 4) traverses a rocky slope and entailed a 30 m elevation gain over a distance of 500 m; at least 80% of the route was over land.

Growth of Adult Frogs.—Adult frogs caught at Sixty Lake Basin donor area did not differ significantly in length between 1994 and 1995 (SVL 5.6 vs. 5.5 cm), but they weighed significantly more in 1994 (18.5 vs. 14.7 g, Mann-Whitney $U = 3545$, $n = 143$, $P < 0.001$). A comparison of weight/length^3 shows that the 1994 frogs had significantly (19%) higher values than 1995 frogs ($U = 3970$, $n = 143$, $P < 0.001$). At the Tableland release sites in 1995, almost all frogs gained weight after repatriation. Average weight gain at the three release sites ranged from 22 to 28%, with an average of 24% (Wilcoxon $T = 1$, $n = 47$, $P < 0.001$). We recorded a similar, significant increase in length at all three sites combined (~2 mm; $T = 32$, $n = 47$, $P < 0.001$). On 20 September 1995, the condition (weight/length^3) of translocated frogs had significantly increased (by 19%) since their original capture on 25 August 1995 (0.095 g/cm^3 versus 0.085 g/cm^3; $T = 84$, $n = 47$, $P < 0.001$).

Predation.—We recorded 168 occurrences of potential predators at the release sites. These included 92 observations of Brewer's Blackbirds (*Euphagus cyanocephalus*), 39 of Western Terrestrial Garter Snakes (*Thamnophis elegans*), 23 of humans (who might catch frogs), and four or fewer observations of Common Ravens (*Corvus corax*), Eared Grebes (*Podiceps nigricollis*), American Dippers (*Cinclus mexicanus*), American Kestrels (*Falco sparverius*), Black Bears (*Ursus americanus*), Coyotes (*Canis latrans*), and Northern Alligator Lizards (*Elgaria coerulea*). Blackbirds appeared to be preying on insects; we never saw them eating anything as large as a *R. muscosa* tadpole. Of the 32 garter snakes caught and palpated, five had eaten larval or subadult *R. muscosa*. All garter snakes were recorded at the three Tableland sites where repatriated *R. muscosa* disappeared most rapidly. None were at Far Pond, where *R. muscosa* persisted the longest. All but four of the snakes were observed in 1994.

Amongst the birds, only the Eared Grebe seemed to have the potential to have an impact on *R. muscosa* because that species has been reported to eat both tadpoles and small frogs (http://www.houghtonmifflinbooks.com/peterson/resources/identifications/eagr/index.shtml#feeding and http://sdakotabirds.com/species/eared_grebe_info.htm). In

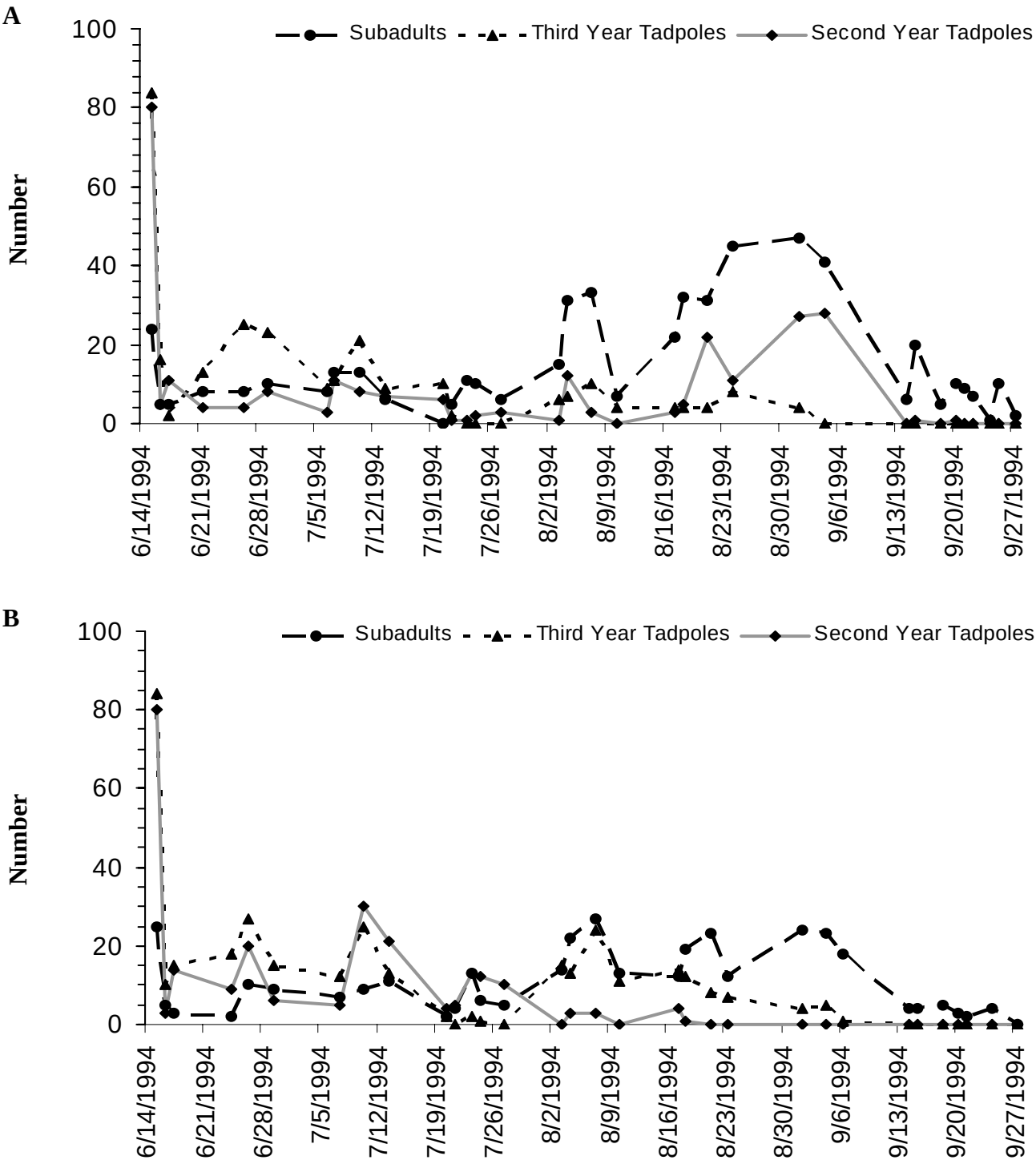


FIGURE 6. Counts of *Rana muscosa* at Frog Lake (A) and Table Meadow (B) and the adjacent dispersal ponds, Sequoia National Park, in 1994. Egg masses, second-year tadpoles, third-year tadpoles, and subadult frogs were released on 14 June 1994. The number graphed for that day represents the actual number released. See Table 1 for numbers of each life history stage repatriated.

1995, an Eared Grebe was seen at Full Moon Pond during three consecutive surveys (27 and 28 September and 4 October). We used binoculars to observe approximately 60 dives during a one-hour period. Only once did the grebe appear to surface with something in its beak that might have been a frog or tadpole.

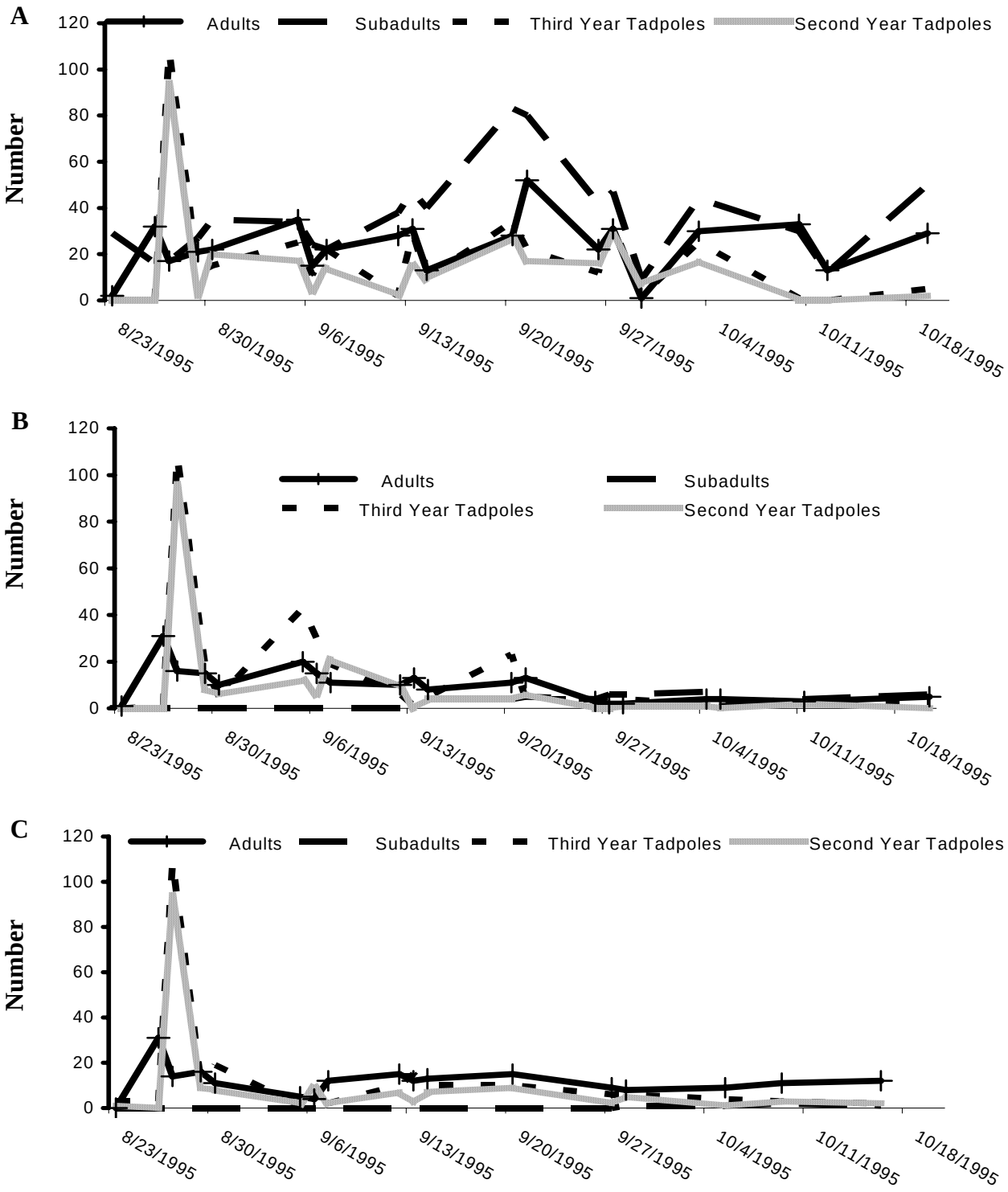
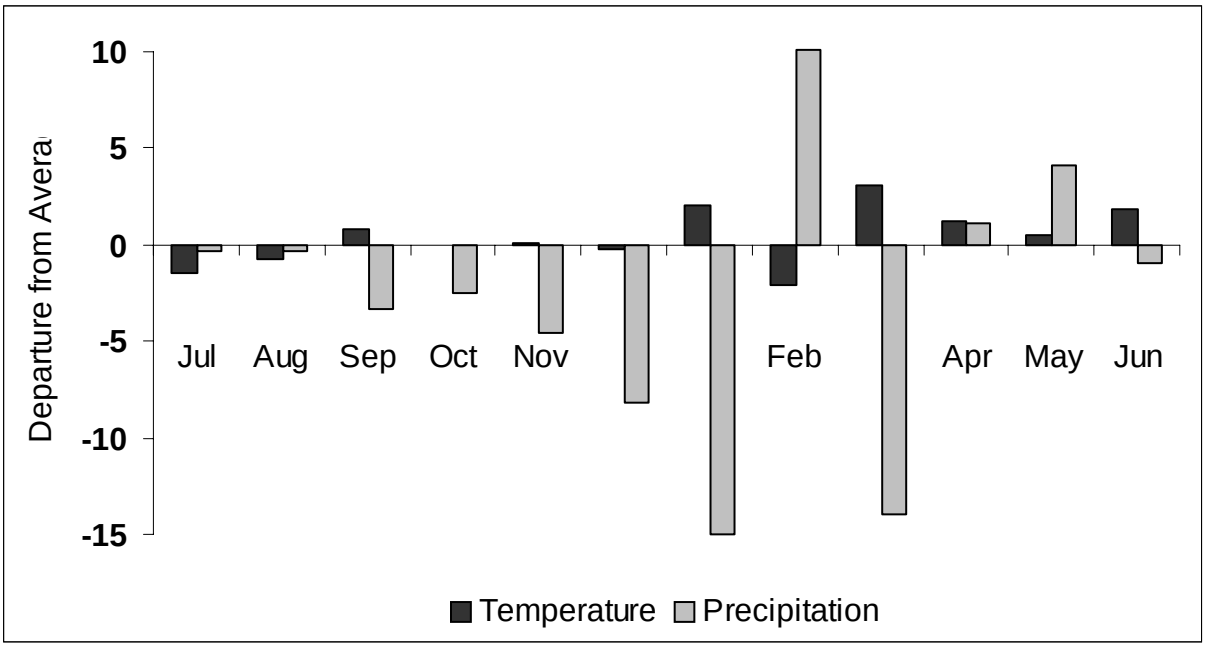


FIGURE 7. Counts of *Rana muscosa* at Far Pond (A), Full Moon Pond (B), and Frog Lake (C) and the adjacent dispersal ponds, Sequoia National Park, in 1995. Second-year tadpoles, third-year tadpoles, and adult frogs were released on 26 August 1995. See Table1 for the numbers and dates of repatriation for each life history stage in 1994 and 1995.

Environmental Measurement.—During 1994, pH varied little from week to week; most values were between 6.0 and 7.0 (mean = 6.5 $\pm$ 0.4, range 5.7-7.8, n = 59). We observed no seasonal trend (linear regression, $R^2 = 0.0074$, $T = 1.15$, $P = 0.25$). In 1995, pH ranged from 6.02 to 7.01 (mean = 6.5 $\pm$ 0.3, n = 34), and showed a slight rise

A.



B.

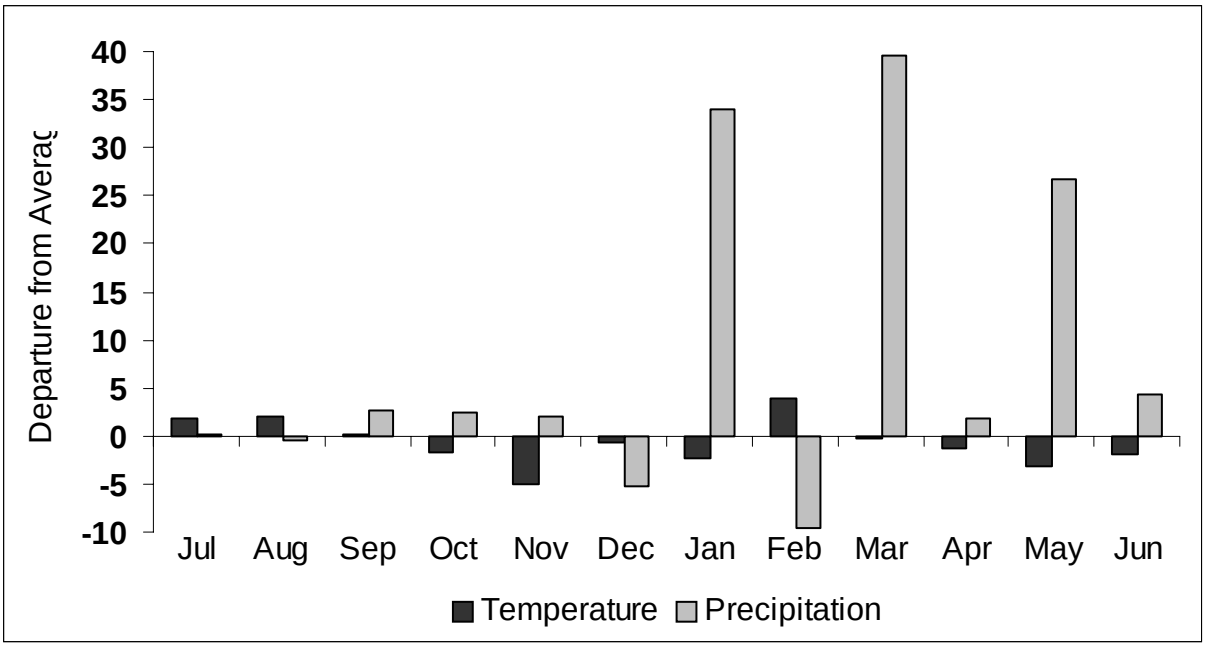


FIGURE 8. Departures from normal (long-term average) temperature and precipitation for 1993 - 1994 (A) and 1994-1995 (B) as measured at Grant Grove, CA (32 km NW of the Tablelands). Temperature is degrees C and precipitation is in centimeters.

through the summer. Conductivity (an indication of the quantity of dissolved electrolytes) was mostly between 2 and 10 µS/cm (mean = 5.2 $\pm$ 4.5, range 1.5-32, n = 93). Conductivity was significantly lower in 1995, a year of high precipitation (98 cm above normal), than in 1994, a year of low precipitation (34 cm below normal; National Weather Service, Grant Grove, CA) (T = 5.53, P < 0.001, n = 93). Conductivity values were lower in Far Pond and Full Moon Pond, at the tops of their watersheds (mean = 3.0, n = 46), than they were in Frog Lake and the Table Meadow stream (mean = 7.3, n = 47), farther down in their watersheds in 1994-95 (T = 6.6, P < 0.001). Values increased during each summer as snowmelt runoff decreased. The highest values were found in the Table

Meadow stream late in the 1994 season, when stream flow had almost stopped.

By early January 1995, water temperature at the Far Pond shallow data logger had cooled to a constant 0 C, indicating freezing to that depth. By mid-January, the deep data logger had also cooled to 0 C. Both remained at zero until the unusually late thaw that began in August 1995. Surface temperatures during the 1995-1996 winter at Far Pond, Full Moon Pond, and Frog Lake indicated that the ponds froze at the surface between late-November and early-December, and remained frozen until late June to early July 1996. Data from the benthic data loggers showed that none of the three ponds froze to the bottom during that winter. The two shallower ponds (Full Moon Pond and Far Pond) cooled to less than 4 C.

Pesticide analysis.—In frog tissues, dichlorodiphenyldichloroethylene (DDE) concentration was one to two orders of magnitude higher than the other organochlorines (Table 3). Both γ-chlordane and trans-nonachlor were found in significantly greater concentrations in Tableland frog tissues compared with Sixty Lakes (Fellers et al. 2004). Organophosphate insecticides (chlorpyrifos and diazinon) were observed primarily in surface water, with higher concentrations at the Tableland sites (Table 4). No contaminants were found at significantly higher concentrations in our Sixty Lakes samples.

DISCUSSION

***Loss of* Rana muscosa**.—Both frogs and tadpoles repatriated to the Tableland area appeared to grow and develop normally. Adult *R. muscosa* showed substantial weight gain and a small increase in length. At three ponds in 1994, and at Far Pond in 1995, metamorphosis of tadpoles occurred since the maximum number of subadults substantially exceeded the number repatriated at the start of the season. Metamorphosis continued into 1996, particularly at Far Pond. These observations indicate that survival and successful development of third-year tadpoles occurred through metamorphosis.

In spite of the growth of adults and development of tadpoles, long-term survival of *R. muscosa* was poor, and there was only limited reproduction. While the number of subadults increased initially in both 1994 and 1995 as a result of metamorphosis, the number of subadult frogs declined by the end of each year. With the exception of Far Pond, there was almost no survival of subadults through the winter. Adult survival was also poor; adults disappeared precipitously at Full Moon Pond and Frog Lake, and more slowly at Far Pond. The only evidence of reproduction was at Far Pond, where we found a few first-year tadpoles in 1995, and a single second-year tadpole in 1998, three years after the last second-year tadpole had been released.

The lack of significant survival or reproduction indicates that the Tableland sites were not suitable for *R. muscosa* in the mid-1990s. Whatever caused the disappearance of *R. muscosa* from the Tableland during the late 1970s and 1980s may also have inhibited the survival of *R. muscosa* 10-15 years later. Other studies have shown that repatriations of *R. muscosa* can be successful if the factor causing the original decline has been eliminated. For example, in August 2001, Roland Knapp (pers. comm.) repatriated 10 adult *R. muscosa* and 200 tadpoles into a lake in the Humphrey's Basin in the Sierra Nevada where introduced trout had been removed. By late 2002, the frog population consisted of approximately 100 frogs and 300 first year tadpoles. This demonstrated that the relatively small number of adults he used in the initial introduction was sufficient to allow establishment of a new population, at least over the short term. Unfortunately, the population was subsequently extirpated because of a die-off apparently caused by the chytrid fungus *B. dendrobatidis* (Knapp, pers. comm.). However, as Dodd and Seigel (1991) and Dodd (2005) point out, most attempts at repatriation do not result in sustainable populations.

***Possible Causes for the Loss of* Rana muscosa**.—Any explanation of the failure to reestablish *R. muscosa* populations by 1997 must account for both the conspicuous disappearance of adults and subadults, and the minimal amount of reproduction. Data on dispersal, weather, water quality, predation, disappearance of individuals by life stage, and contaminants were used to evaluate potential causes of decline. Fortunately, our study site was in a fishless area, so the impact of non-native trout was not a factor as it is throughout most of the Sierra Nevada (Vredenburg 2004).

The most conspicuous deviation from normal weather patterns during our study was the winter of 1994-1995 (Fig. 8). Conditions were similar to the winter of 1977-1978 when adult *R. muscosa* did not survive the winter at any of the three repatriation ponds in our study (Bradford 1983). Those die-offs were attributed to winterkill due to oxygen depletion in the water. Disappearance of both adults and subadults from Full Moon Pond and Frog Lake during the winter of 1994-1995 may have occurred for this reason. Unusual temperatures and precipitation were not evident during the 1995-1996 winter, and thawing at the release sites occurred in late June to early July. Consequently, winterkill due to oxygen depletion or freezing was not likely to be responsible for the loss of adults and subadults during the 1995-1996 winter. Moreover, this does not account for the much greater survivorship of these life stages at Far Pond (our highest elevation site) than the other two sites during the winters of both 1994-1995 and 1995-1996.

Lakes in the Sierra Nevada have low buffering capacity and hence are susceptible to acidification (Melack et al. 1985; Landers et al. 1987). Sierran lakes are also low in

ionic strength (Landers et al. 1987) and low pH levels would be expected to cause the most physiological stress at low ionic strengths (Freda and Dunson 1984). While our EC values were low compared with other Sierran lakes (Eilers et al. 1987; Bradford et al. 1994b; J. Sickman, pers. comm.), it is unlikely that the EC and pH were deleterious to *R. muscosa.* In a study of amphibian habitats at high elevations throughout the Sierra Nevada, Bradford et al. (1994b) found no association between the presence/absence of *R. muscosa* at a site and the pH or EC of the water. Moreover, the pH and EC values observed by Bradford et al. at sites inhabited by *R. muscosa* (e.g., minimum pH = 5.6, minimum EC = 3 μS/cm) included or were close to the values observed in our study (minimum pH = 5.6, minimum EC = 2 μS/cm).

Predators may have been a minor contributing factor in the loss of *R. muscosa*. In 1994, Western Terrestrial Garter Snakes were common at Table Meadow, Frog Lake, and Full Moon Pond. Five of 32 garter snakes contained the remains of *R. muscosa*. This included three of six snakes captured at Frog Lake, two of 18 at Full Moon Pond, and zero of eight at Table meadow; we never observed snakes at Far Pond. The lack of snakes at Far Pond might have been because that pond was in a granite basin with little vegetation. The three sites that did support snakes had historically supported large populations of *R. muscosa*. Garter snakes occur throughout the range of *R. muscosa*, but they occur almost exclusively at sites where either *R. muscosa* or *Pseudacris regilla* are present (Jennings et al. 1992; Matthews et al. 2002). Thus, the presence of this native snake is unlikely to be the primary cause of the loss of *R. muscosa*, especially because snakes would be inactive during winter when many adult and subadults disappeared. Though a single grebe was seen at two of the release sites, Full Moon Pond and Frog Lake, it is unlikely that foraging by one individual would be the primary factor leading to the loss of frogs.

Of the 143 adult *R. muscosa* released at the Tableland sites, at least 22 (15.4%) dispersed to nearby ponds or streams, but dispersal alone is unlikely to account for the loss of frogs, particularly during winter. Matthews and Pope (1999) evaluated movement of 24 *R. muscosa* using radio transmitters. They found that movement varied seasonally with the greatest movement occurring in September (mean distance moved = 145 m), and the least movement at the onset of winter dormancy during October (43 m). These distances are similar to what we observed in the Tableland area; hence, it does not seem that dispersal from the release sites is a likely cause of the loss of frogs, especially considering that frogs were getting sick and dying at the release sites.

Infection by the chytrid fungus *B. dendrobatidis* is a plausible cause for the loss of *R. muscosa* in the Tableland, both during the 1970s and 1980s, and during our experimental reintroduction in the 1990s. Prior to 1998, it was thought that chytrid fungi did not infect vertebrate hosts. In 1998, Berger et al. (1998) described chytrid infections in frogs. Several subsequent studies provided strong correlative evidence that *B. dendrobatidis* was involved with declines in frog populations in both Panama (Lips 1999) and Australia (Berger et al. 1998). Fellers et al. (2001) reported *B. dendrobatidis* in *R. muscosa* from the Sierra Nevada, less than 150 km north of the Tableland area. Recently, Rachowicz et al. (2006) demonstrated through extensive field surveys and laboratory and field experiments that chytridiomycosis was the proximate cause of numerous observed *R. muscosa* population declines in the southern Sierra Nevada. A conspicuous finding was that post-metamorphic stages of *R. muscosa* experience high mortality from chytrid infection, whereas tadpoles do not. Tadpoles infected with *B. dendrobatidis* survive to metamorphosis, but typically succumb to chytrid infection shortly after metamorphosis. This pattern is consistent with the die-offs and disappearances of adults, subadults, and recently metamorphosed frogs that were observed in the Tableland in the 1970s (Bradford 1983, 1991), as well as during the present study. Since chytrid infection of frogs was not described until after our study, we did not look for it during our experimental repatriation.

Bradford (1991) reported a massive die-off of *R. muscosa* in a Tableland population during the summer of 1979 that appeared to be caused by red-leg disease, an infection caused by the bacteria *Aeromonas hydrophila*. Carey et al. (1999) suggested that the 1979 die-off may have been caused by *B. dendrobatidis* and that the bacterial infections were secondary, a hypothesis that cannot be tested today. *Aeromonas* is unlikely to be involved with the loss of repatriated *R. muscosa* during our study since we found no evidence of this disease (reddening of the thighs) in any of the frogs we handled.

Viral infections have been reported in *Rana aurora* (Mao et al. 1999). Die-offs caused by ranavirus typically kill only tadpoles and recently metamorphed (30-60 days) individuals, and there are often hundreds of dead tadpoles present at a site. By contrast, chytridiomycosis affects only adult anurans, often with only one or a few dead individuals present at a site (David E. Green, pers. comm.). The extent of viral infections in California amphibians is unknown, but a large die-off of *R. muscosa* tadpoles in Kings Canyon National Park in 2001 appears to have been caused by an iridovirus (Roland Knapp, pers. comm.). The significance of viral infections in declining amphibian populations remains largely unknown, but it does not appear to have been a factor in our study because we never observed tadpole die-offs.

Exposure to airborne pesticides is a possible cause for the Tableland population declines. Davidson and Knapp (2007) evaluated over 6800 sites in the southern Sierra Nevada for the presence of *R. muscosa*, the presence of introduced game fishes, habitat conditions, and the predicted exposure to windborne pesticides applied in upwind agricultural areas. In a multivariate analysis,

predicted exposure to pesticides had a pronounced negative effect on *R. muscosa* site occupancy, independent of other factors. This pattern is corroborated by our comparison of frogs from sites in the Tableland (an area near the Central Valley that has high predicted pesticide exposure) and frogs from Sixty Lake Basin (an area more remote from the Central Valley that has low predicted pesticide exposure). When the survival of *R. muscosa* in the Tableland area seemed unlikely in 1997 and most of the remaining frogs appeared sick, the last 20 *R. muscosa* were collected so pesticide concentrations could be compared with a similar set of frogs collected at the Sixty Lake Basin donor sites. Several pesticides, especially pp-DDE, were found at higher concentrations in frog tissue from the Tableland sites (Fellers et al. 2004).

Based on traditional toxicological studies that expose animals to contaminants for only brief periods of time (24-96 hr), it seems unlikely that the loss of *R. muscosa* was caused by the relatively low concentration of pesticides that have been found in the Tableland area. However, Relyea and Mills (2001) showed that increasing contaminant exposure from four to 10 days caused a significant increase in mortality. Thus, some of the contaminants in the Tableland may be present in concentrations sufficiently high to account for the loss of frogs. This is especially true for *R. muscosa* because they typically require three years for tadpoles to metamorphose, and 3-4 years for frogs to reach sexual maturity (Vredenburg et al. 2005). This means that *R. muscosa* tadpoles are exposed to contaminants in the water for an usually long time, possibly allowing them to accumulate more contaminants and making them (or the subsequent adults) more vulnerable (Sparling et al. 2001). In addition, it has been suggested that pesticide exposure may affect amphibian populations by suppressing immune function, thus making amphibians more susceptible to disease (Davidson and Knapp 2007).

While we did not identify the specific cause for either the original or subsequent loss of *R. muscosa* in the Tableland area of the Sierra Nevada, the evidence is compatible with chytridiomycosis and contaminants as a primary cause of the decline. Either one of these factors, or the two acting in concert, may have made the Tableland area unsuitable for *R. muscosa*. Hopefully, ongoing research on *R. muscosa* and other anurans in the Sierra Nevada will help elucidate this situation and allow for reestablishment of viable *R. muscosa* populations.

***Acknowledgment*s**.—Bruce Christman, Jennifer Ellingson, Craig Fellers, Scott Fellers, Kathleen Freel, and Mark Massar assisted with the field work. Annie Esperanza, David Graber, Janie McLaughlin, and Harold Werner provided logistical support. Roberta Larson assisted with data processing. Joan Fellers and Patrick Kleeman provided useful comments on the manuscript. The research was funded by the National Park Service. Sequoia and Kings Canyon National Parks, and the California Department of Fish and Game provided collecting permits. The U.S. Environmental Protection Agency (EPA), through its Office of Research and Development, collaborated in this project. The document has undergone EPA review and has been approved for publication. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

LITERATURE CITED

Berger, L., R. Speare, P. Daszak, D.E. Green, A.A. Cunningham, C.L. Goggin, R. Slocombe, M.A. Ragan, A.D. Hyatt, K.R. McDonald, H.B Hines, K.R. Lips, G. Marantelli, and H. Parkes. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. Proceedings of the National Academy of Sciences USA 95:9031-9036.

Bradford, D.F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. Ecology 64:1171-1183.

_____. 1989. Allotropic distribution of native frogs and introduced fishes in high Sierra Nevada Lakes of California: Implication of the negative effect of fish introductions. Copeia 1989:775-778.

_____. 1991. Mass mortality and extinction in a high-elevation population of *Rana muscosa*. Journal of Herpetology 25:174-177.

_____, C. Swanson, and M.S. Gordon. 1992. Effects of low pH and aluminum on two declining species of amphibians in the Sierra Nevada, California. Journal of Herpetology 26:369-377.

_____, M.S. Gordon, D.F. Johnson, R.D. Andrews, and W.B. Jennings. 1994b. Acidic deposition as an unlikely cause for amphibian population declines in the Sierra Nevada, California. Conservation Biology 69:155-161.

_____, D.M. Graber, and F. Tabatabai. 1994a. Population declines of the native frog, *Rana muscosa*, in Sequoia and Kings Canyon National Parks, California. Southwestern Naturalist 39:323-327.

Carey, C., N. Cohen, and L. Rollins-Smith. 1999. Amphibian declines: An immunological perspective. Developmental and Comparative Immunology 23:459-472.

Crump, M.L., and N.J. Scott, Jr. 1994. Visual encounter surveys. Pp. 84-91 *In* Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Heyer, W.R., M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster (Eds.). Smithsonian Institution Press, Washington, DC, USA.

Davidson, C., and R. A. Knapp. 2007. Multiple stressors and amphibian declines: dual impacts of pesticides and fish on yellow-legged frogs. Ecological Applications 17:587-597.

Dodd, C.K., Jr. 2005. Amphibian conservation and population manipulation. Pp. 265-270 *In* Status and Conservation of U.S. Amphibians. Lannoo, M.J. (Ed.). Vol. 1: Conservation Essays. University of California Press, Berkeley, California, USA.

Dodd, C.K., Jr. and R.A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47:336-350.

de Bruijn, J., F. Busser, W. Seinen, and J. Hermens. 1989. Determination of octanol/water partition coefficients for hydrophobic organic chemicals with the "slow-stirring" method. Environmental Toxicology and Chemistry 8:499-512.

Eilers, J.M., P. Kanciruk, R.A. McCord, W.S. Overton, L. Hook, D.J. Blick, D.F. Brakke, P.E. Kellar, M.S. DeHaan, M.E. Silverstein, and D.H. Landers. 1987. Western Lake Survey Phase I. Characteristics of lakes in the western United States. Vol. II. Data compendium for selected physical and chemical variables. EPA-600/3-86/054b.

Fellers, G.M., and K.L. Freel. 1995. A standardized protocol for surveying aquatic amphibians. U.S. Department of Interior, National Park Service Technical Report NPS/WRUC/NRTR-95-01. 117 p.

_____, L.L. McConnell, D. Pratt, and S. Datta. 2004. Pesticides in mountain yellow-legged frogs (*Rana muscosa*) from the Sierra Nevada Mountains of California, USA. Environmental Toxicology and Chemistry 23:2170-2177.

Filippi, E., L. Rugiero, M. Capula, D. Capizzi, and L. Luiselli, L. 2005. Comparative food habits and body size of five populations of *Elaphe quatuorlineata*: the effects of habitat variation, and the consequences of intersexual body size dimorphism on diet divergence. Copeia 3:517-525.

Finizio, A., M. Vighi, and D. Sandroni. 1997. Determination of n-octanol/water partition coefficient (K_{ow}) of pesticide critical review and comparison of methods. Chemosphere 34:131-161.

Freda, J., and W.A. Dunson. 1984. Sodium balance of amphibian larvae exposed to low environmental pH. Physiological Zoology 7:435-443.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183-190.

Grinnell, J., and T.I. Storer. 1924. Animal Life in the Yosemite. University of California Press, Berkeley, California, USA.

Jennings, W.B., D.F. Bradford, and D. Johnson. 1992. Dependence of the garter snake *Thamnophis elegans* on amphibians in the Sierra Nevada of California. Journal of Herpetology 26:503-505.

Knapp, R.A., and K.R. Matthews. 2000. Non-native fish introductions and the decline of the Mountain Yellow-legged Frog from within protected areas. Conservation Biology 14:428-438.

Landers, D.H., J.M. Eilers, D.F. Brakke, W.S. Overton, P.E. Kellar, M.E. Silverstein, R.D. Schonbrud, R.E. Crowe, R.A. Linthurst, J.M. Omernik, S.A. Teague, and E.P. Meier. 1987. Western Lake Survey Phase I. Characteristics of Lakes in the Western United States. Volume I: Population descriptions and physico-chemical relationships. EPA/600/3-86/054a. 178 p.

LeNoir, J.S., L.L. McConnell, G.M. Fellers, T.M. Cahill, T.M., and J.N. Seiber. 1999. Summertime transport of current-use pesticides from California's Central Valley to the Sierra Nevada Mountain Range, USA. Environmental Toxicology and Chemistry 18:2715-2722.

Lips, K.R. 1999. Mass mortality and population declines in anurans at an upland site in western Panama. Conservation Biology 13:117-125.

Mao, J., D.E. Green, V.G. Chinchar, and G.M. Fellers. 1999. Molecular characterization of iridoviruses isolated from sympatric amphibians and fish. Virus Research 63:45-52.

Matthews, K.R., and K.L. Pope. 1999. A telemetric study of the movement patterns and habitat use of *Rana muscosa*, the Mountain Yellow-legged Frog, in a high-elevation basin in Kings Canyon National Park, California. Journal of Herpetology 33:615-624.

_____, R.A. Knapp, and K.L. Pope. 2002. Garter snake distributions in high-elevation aquatic ecosystems: Is there a link with declining amphibian populations and nonnative trout introductions? Journal of Herpetology 36:16-22.

Melack, J.M., J.L. Stoddard, and C.A. Ochs. 1985. Major ion chemistry and sensitivity to acid precipitation of Sierra Nevada lakes. Water Resources Research 21:27-32.

Pope, K.L., and K.R. Matthews. 2001. Movement ecology and seasonal distribution of Mountain Yellow-legged Frogs, *Rana muscosa*, in a high-elevation Sierra Nevada basin. Copeia. 2001:787-793.

Rachowicz, L.J., R.A. Knapp, J.A.T. Morgan, M.J. Stice, V.T. Vredenburg, J.M. Parker, and C.J. Briggs. 2006. Emerging infectious disease as a proximate cause of amphibian mortality. Ecology 87:1671-1683.

Relyea R., and N.N. Mills. 2001. Predator-induced stress makes the pesticide carbaryl more deadly to Gray Treefrog tadpoles (*Hyla versicolor*). Proceedings of the National Academy of Sciences USA 98:2491-2496.

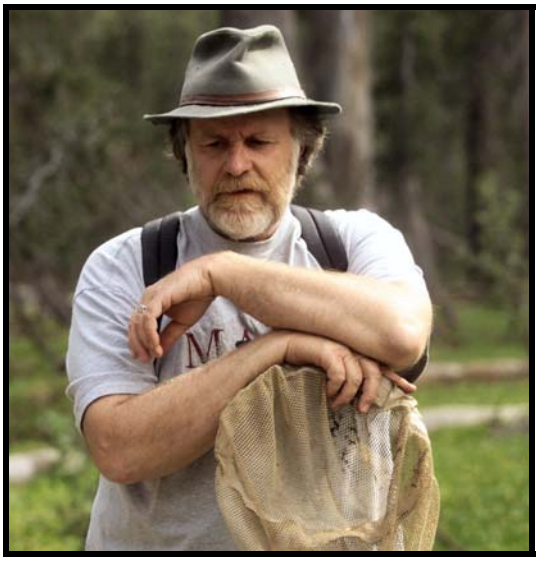
Sparling, D.W., G.M. Fellers, and L.L. McConnell. 2001. Pesticides and amphibian population declines in California, USA. Environmental Toxicology and Chemistry 20:1591-1595.

Suntio, L.R., W.Y. Shiu, D. Mackay, J.N. Seiber, and D. Glotfelty. 1988. Critical reviews of Henry's Law constants for pesticides. Reviews of Environmental Contamination and Toxicology 103:1-59.

Vredenburg, V.T. 2004. Reversing introduced species effects: Experimental removal of introduced fish leads to rapid recovery of a declining frog. Proceedings of the National Academy of Sciences 101:7646-7650.

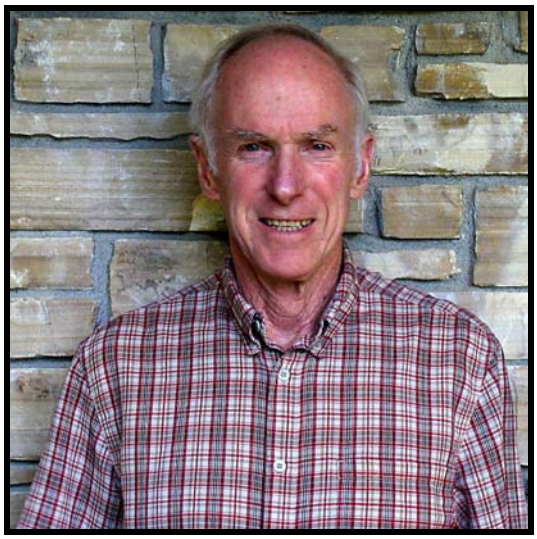
Vredenburg, V., G.M. Fellers, and C. Davidson. 2005. *Rana muscosa* Camp 1917, Mountain Yellow-legged Frog. Pp. 563-566 *In* Amphibian Declines: The Conservation Status of United States Species. Lannoo, M. (Ed.). University of California Press, Berkley, California, USA.

Zweifel, R.G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylei* group. University of California Publications in Zoology 54:207-292.



GARY M. FELLERS is a Research Biologist for the U.S. Geological Survey, Western Ecological Research Center and is stationed at Point Reyes National Seashore. He received B.S. in Biology from the University of California at Berkeley, a M.S. in zoology from the University of Michigan, and a Ph.D. in zoology from the University of Maryland. Gary has conducted research on a variety of plants and animals including the breeding behavior of treefrogs, tool use in ants; population status of rare plants, distribution of Argentine ants in Hawaii, and the ecology of island night lizards, island foxes, and spotted skunks on the Channel Islands off southern California. His current research includes the ecology island night lizards, and the population status and causes of decline of amphibians throughout the non-desert portions of California.

David F. Bradford is a Research Ecologist in the Landscape Ecology Branch, Office of Research and Development, U.S. Environmental Protection Agency in Las Vegas, Nevada. He received a BA in Biology from Fresno State University, MA in Zoology from the University of California at Berkley, and Ph.D. in Biology from UCLA. His current research interests focus on interactions between landscape patterns, habitat and stressor distributions, and animal distributions. He has investigated a number of possible causes for amphibian population declines in the western US, including acid deposition, invasive species, UV radiation, habitat fragmentation, and airborne pesticides.



David Pratt is a retired biologist. Initially, he retired from a career as a microbiologist at the University of Wisconsin and the University of California at Davis. He subsequently worked as a wildlife biologist for the U.S. Forest Service, National Park Service, and U.S. Geological Survey before retiring for a second time. He has participated in research on pine martens in California, Washington, and Colorado; willow flycatcher nesting preferences in the sierra foothills; spotted owl surveys in the Sierra Nevada; small mammal, mesocarnivore, amphibian, and reptile inventories at Point Reyes National Seashore; and vegetation analysis of black oak woodlands in the sierra foothills.

LESLIE LONG WOOD is an independent consultant who works on projects involving California amphibians and birds, particularly California red-legged frogs. She received a B.S. in zoology from the University of California at Davis and an M.S. in marine science from the University of California at Santa Cruz. She has conducted research on the effects of pH and UV-B on amphibians, and has participated in research projects involving spotted frogs in Idaho, amphibian distribution in California, foothill yellow-legged frogs in the Sierra foothills, California red-legged frogs at Point Reyes, Guadalupe fur seals on Guadalupe Island, Baja California, Mexico, and oceanographic research in the Weddell Sea, Antarctica.