Rana muscosa Camp, 1917(b)

MOUNTAIN YELLOW-LEGGED FROG

Vance Vredenburg, Gary M. Fellers, Carlos Davidson

1. Historical versus Current Distribution. Mountain yellow-legged frogs (*Rana muscosa*) are endemic to two disjunct areas: (1) the Sierra Nevada in California and Nevada, and (2) the San Gabriel, San Bernardino, and San Jacinto Mountains in southern California. This species was originally described as two subspecies of *Rana boylii* (*Rana boylii muscosa* and *R. boylii sierrae*; Camp, 1917b). On the basis of morphological data, the two subspecies were separated from *R. boylii* and raised to the species level (*R. muscosa*; Zweifel, 1955). Recent molecular data (Macey et al., 2001) suggest that there may be large differences between the frogs in these two disjunct areas; therefore, we will refer to Sierran populations and southern California populations separately whenever possible.

In the Sierran range, mountain yellow-legged frogs occur from near Antelope Lake (northern Plumas County; G.M.F., in preparation), south 490 km to Taylor Meadow (southern Tulare County; Zweifel, 1955) and range from 1,370–3,660 m (Camp, 1917b; Grinnell and Camp, 1917b; Storer, 1925; Zweifel, 1955; Mullally and Cunningham, 1956). They are not known from east of the Sierra Crest except for two regions: in the vicinity of Mt. Rose, near Lake Tahoe (Zweifel, 1955) where populations are now extirpated, and in the Glass Mountains south of Mono Lake, where there are two small populations. Currently, mountain yellow-legged frogs are found scattered throughout nearly all their historical range in Sierra Nevada, but the number of populations is greatly reduced. This is most notable in the northernmost 125 km of the range (north of Lake Tahoe) and the southernmost 50 km, where only a few populations have been found in the last few years (see "Historical versus Current Abundance" below; Jennings and Hayes, 1994a; G.M.F., in preparation).

In southern California, the historical range included the San Gabriel, San Bernardino, and San Jacinto Mountains with an isolated population at Mt. Palomar (in northern San Diego County; Camp, 1917b) and ranged from 300–2,300 m (Camp, 1917b; Grinnell and Camp, 1917; Storer, 1925; Zweifel, 1955). The frogs were thought to have gone extinct in the San Bernardino Mountains (none were found between 1970–'93; Jennings and Hayes, 1994a), but a small population was recently discovered (M. Jennings, personal communication). In the southern California portion of their range, nearly all populations of mountain yellow-legged frogs have disappeared (Jennings and Hayes, 1994a; see below) and, given their status as a distinct vertebrate population segment, were given Endangered species as of 1 August 2002 (U.S.F.W.S., 2002b).

2. Historical versus Current Abundance. A large number of Sierran populations have disappeared, but the extent of decline is unclear due to the lack of systematic surveys (Jennings and Hayes, 1994a). Between 1989–'93, Bradford et al. (1994a) resurveyed mountain yellow-legged frog "historical sites" (documented between 1959–'79). In the western portion of Sequoia National Park (Kaweah River drainage), they resurveyed 27 historical sites and found no frogs at any of these locations (Bradford et al., 1994a). Elsewhere in Sequoia and Kings Canyon National Parks (Kern, Kings, and San Joaquin River drainages), they resurveyed 22 historical sites and only 11 contained frogs (Bradford et al., 1994a). Beginning just north of Kings Canyon National Park and running up into Yosemite National Park, they resurveyed 24 historical sites and found frogs present at only 3 sites (Bradford et al., 1994a). In another study, Drost and Fellers (1996) compared the presence of Sierran mountain yellow-legged frogs at historical sites (surveyed in 1915 by Grinnell and Storer) to distributions in 1995. Grinnell and Storer (1924) stated that "the yellow-legged frog is the commonest amphibian in most parts of the Yosemite section." Drost and Fellers (1996) report finding frogs in only 2 of 14 historical sites (a single tadpole at one site, and an adult female at another). If we combine the data from the two resurvey studies in the Sierra Nevada (Bradford et al., 1994a; Drost and Fellers, 1996), there are 86 historical sites (data from 1915–'59), and only 16 contained frogs when they were revisited between 1989–'95. At the northernmost and southernmost part of the Sierran range (Butte and Plumas counties in the north, and Tulare County in the south), few populations have been seen since 1970 (Jennings and Hayes, 1994a; G.M.F., in preparation).

In southern California, mountain yellow-legged frog populations have declined nearly to extinction (Jennings and Hayes, 1994a; Stebbins and Cohen, 1995; Drost and Fellers, 1996; U.S.F.W.S., 2002b). With only 6–8 extant populations, the largest having fewer than 100 adults (M. Jennings, personal communication), the situation is tenuous at best for mountain yellow-legged frogs in southern California.

3. Life History Features.

A. Breeding. Reproduction is aquatic.

i. Breeding migrations. Sierran mountain yellow-legged frogs do not have a distinct breeding migration because adults spend most of their time in the vicinity of suitable breeding habitat (Zweifel, 1955; Bradford, 1983). In some areas, there is a seasonal movement from lakes that are more favorable for overwintering (e.g., deeper water, see "Torpor" below) to nearby areas that are more favorable for breeding. Frogs typically move only a few hundred meters, but distances up to 1 km have been observed (V.V., in preparation). Breeding activity begins early in the spring, soon after ice-melt, and can range from April at lower elevations to June–July in higher elevations (Wright and Wright, 1933; Stebbins, 1951; Zweifel, 1955). The timing of the onset of breeding is dependent upon the amount of snowfall and subsequent ice-out dates of ponds, lakes, and streams (V.V., in preparation).

Almost no data exist on dispersal of juvenile mountain yellow-legged frogs from either Sierran populations (Bradford, 1991) or southern California. In the Sierra Nevada, juveniles have been observed in small intermittent streams and may have been dispersing to permanent water (Bradford, 1991). Although it has been reported that frogs avoid crossing even short distances of dry ground (Mullally and Cunningham, 1956), we have documented overland movement of Sierran frogs well away from water (≤ 400 m; Vredenburg and Fellers, in preparation).

ii. Breeding habitat. Southern California populations are almost exclusively stream-dwelling, perhaps reflecting the general lack of ponds and lakes in the area. It is not known whether southern California populations overwinter as tadpoles before metamorphosis, therefore, the restriction for breeding habitat to deeper, more permanent bodies of water (or habitats connected to them) may not apply to these populations.

B. Eggs.

i. Egg deposition sites. In Sierran populations, eggs are deposited underwater in clusters under banks or attached to rocks, gravel, or vegetation in streams or lakes (Wright and Wright, 1949; Stebbins, 1951; Zweifel, 1955). In the Sierra Nevada, tadpoles overwinter at least once before metamorphosis (Bradford, 1983; see below). Therefore, egg-laying sites must either be in or connected to lakes and ponds that do not dry in the summer and are sufficiently deep that they do not freeze to the bottom in the winter (> 1.7 m deep, and preferably > 2.5 m deep; Bradford, 1983; see below). Southern California populations are almost exclusively stream dwelling, perhaps reflecting the general lack of ponds in the area. It is not known whether southern California populations overwinter as tadpoles before metamorphosis, therefore the restriction for breeding habitat to deeper, more permanent bodies of water (or habitats connected to them) may not apply to these populations.

ii. Clutch size. Livezey and Wright (1945) report an average of 233 eggs/egg mass (n = 6, range 100–350) for Sierran frogs, but we have observed egg masses with as few as 15 eggs, so the average is probably less (V.V., in preparation). In laboratory breeding experiments on Sierran frogs, egg hatching times ranged from 18–21 d at temperatures ranging from 5–13.5 ˚C (Zweifel, 1955).

C. Larvae/Metamorphosis.

i. Length of larval stage. The length of the larval stage depends upon the elevation. At lower elevations where the summers are longer, tadpoles are thought to be able to grow to metamorphosis in a single season (Storer, 1925). However, throughout most of their

range in the Sierra Nevada, populations are clearly composed of tadpoles of three size classes that may correspond to year classes (G.M.F., in preparation). Hence, metamorphosis would occur at the end of the third summer when the tadpoles are 2.5 yr old (Wright and Wright, 1933; Zweifel, 1955). At higher elevations (> 2,500 m) or after winters where ponds and lakes remain ice-covered for ≥ 9 mo, we believe that tadpoles may not metamorphose until the end of their fourth summer. There is no information on the length of the larval stage in southern California populations.

ii. Larval requirements.

a. Food. Not reported, but tadpoles are most likely herbivorous and detritivorous.

b. Cover. Tadpoles burrow in mud, under rocks, under banks, or into submerged vegetation (Stebbins, 1951). Before the spring overturn (thermal mixing in lakes), Sierran tadpoles remain in the warmer water below the thermocline. After mixing occurs, they move each day from the deeper water where they take refuge at night to warm shallow areas near shore where they aggregate in large numbers (Bradford, 1984). There are no reports from southern California populations.

iii. Larval polymorphisms. None.

iv. Features of metamorphosis. Tadpoles transform in July and August (22–27 mm SVL; Wright and Wright, 1933).

v. Post-metamorphic migrations. Not reported.

D. Juvenile Habitat. Believed to be similar to adults.

E. Adult Habitat. In the Sierra Nevada, adult mountain yellow-legged frogs occupy wet meadows, streams, and lakes; adults typically are found sitting on rocks along the shoreline, usually where there is little or no vegetation (Wright and Wright, 1933). In southern California, mountain yellow-legged frogs occupy streams in narrow rock-walled canyons (Grinnell and Camp, 1917) and streams in the chaparral belt (Zweifel, 1955).

In the Sierra Nevada, most frogs are seen on a wet substrate within 1 m of the water's edge. Both adults and larvae are found most frequently in areas with shallow water, in part because these were the warmest areas (Bradford, 1984). Bradford (1984) reported seeing aggregations of Sierran frogs of up to 58 individuals. Aggregations occurred in the early afternoon in situations where the head and back of individual frogs were in full sunlight.

F. Home Range Size. Using radio tracking, home range size was estimated for Sierran mountain yellow-legged frogs in Kings Canyon National Park (Matthews and Pope, 1999). They used adaptive kernal 90% contours to estimate home range separately by month for August, September, and October 1998. In August, ranges for ten females varied from 19.4–1,028 m^2 (x = 385.5 m^2; s.e. = 113.4 m^2). In September, ranges for seven females varied from 53–9,807 m^2 (x = 5,099 m^2; s.e. = 1,506 m^2), and one female was calculated at 6,990 m^2. In October, the calculated home range for one female was 3.2 m^2; for two males the values were 73 m^2 and 82 m^2. This study was conducted in an area dominated by introduced trout (Matthews and Pope, 1999); it is not known if these calculations reflect mountain yellow-legged frog movements in natural conditions (those that lack all fish predators).

G. Territories. Unknown, but other ranid frogs are well known to defend breeding areas (Wells, 1977). In the Sierra Nevada, where the largest populations remain, aggregations of 2–15 adult frogs (with a maximum of 58) can be seen sunning on warm days (Bradford, 1984; Fellers, in preparation).

H. Aestivation/Avoiding Dessication. None.

I. Seasonal Migrations. See "Breeding migrations" above and Pope and Matthews (2001).

J. Torpor (Hibernation). As the temperatures drop to freezing or below (generally October–November), frogs become inactive for the winter (Zweifel, 1955; Bradford, 1983). Sierran frogs apparently spend the winter at the bottom of lakes or in rocky streams (V.V. and G.M.F., in preparation). One study (Matthews and Pope, 1999) reports Sierran frogs overwintering in rock crevices, but this behavior may be in response to the presence of introduced fish (see "Interspecific Associations/Exclusions" below).

Because most Sierran mountain yellow-legged frogs overwinter in lakes, they require lakes that do not freeze to the bottom (> 1.7 m deep and preferably > 2.5 m deep; Bradford, 1983). In the Sierra Nevada, tadpoles seem better able to survive long winters than juvenile and adult frogs (Bradford, 1983). In 1978, winterkill was responsible for the mortality of all but one Sierran adult in 21 of 26 lakes, while tadpoles survived in all 26 lakes (Bradford, 1983). In laboratory studies, Bradford (1983) confirmed that Sierran mountain yellow-legged tadpoles have a greater tolerance of hypoxia and a reduced consumption of energy and oxygen during hibernation when compared to metamorphosed individuals (juveniles and adults).

In the Sierra Nevada, adults emerge as soon as the ponds and lakes begin to thaw and ice is clear from at least part of the water surface. As with Yosemite toads (*Bufo canorus*), adults sometimes travel over snow to reach preferred breeding sites early in the season. In years with particularly cold winters, high elevation populations (> 3,000 m) of Sierran mountain yellow-legged frogs may only be active for 90 d during the warmest part of the summer (V.V., personal observations).

K. Interspecific Associations/ Exclusions. The native habitat for Sierran populations of mountain yellow-legged frogs is almost entirely outside the range of native fish (Knapp, 1996). This is largely due to the presence of impassable waterfalls in nearly all the Sierran drainages (from past glaciation and uplift processes). Beginning in the late 1800s, trout were introduced to most permanent bodies of water throughout the Sierra Nevada (Knapp, 1996). Accounts of introduced trout eating Sierran mountain yellow-legged frogs go back many years (Grinnell and Storer, 1924; Needham and Vestal, 1938), yet introductions of trout continue throughout much of the Sierran Range (Knapp, 1996). Sierran mountain yellow-legged frogs are found in substantially lower densities in ponds and lakes with trout compared with similar habitats that lack fish (Grinnell and Storer, 1924; Bradford, 1989), and those places of co-occurrence probably represent sink populations of frogs (Bradford, 1989; V.V., in preparation). A recent survey of Sierra Nevada sites comparing 669 bodies of water in U.S. Forest Service land (where fish are still routinely introduced) to 1,059 in National Park Service land (where fish introductions ceased in 1977) showed a dramatic difference in the occurrence of mountain yellow-legged frogs in the two areas (3% and 20%, respectively; Knapp and Matthews, 2000).

Little is known about the effect of introduced trout on southern California populations of mountain yellow-legged frogs. It is clear that trout are playing a substantial role in the declines of Sierran populations; however, there may be multiple explanations. For example, frogs from an entire Sierra Nevada watershed went extinct in an area where trout were never introduced (27 locations; Bradford, 1991).

In a single drainage in the northernmost part of the Sierran range, mountain yellow-legged frogs historically occurred sympatrically with Cascade frogs (*Rana cascadae*) and foothill yellow-legged frogs (*Rana boylii*; Zweifel, 1955). More recently, Stebbins and Cohen (1995) report that all three species of frogs have disappeared from that area; there are now no known sites where all three of these congeners occur together.

In southern California, there are historical accounts of overlap between foothill and mountain yellow-legged frogs along 1.6 km (1 mi) of the North Fork San Gabriel River in Los Angeles County (Zweifel, 1955), but they have both since disappeared from that area (Jennings and Hayes, 1994a). Sierran and southern California mountain yellow-legged frogs continue to co-occur frequently with Pacific treefrogs (*Hyla regilla*; Stebbins, 1985). Rarely, Sierran mountain yellow-legged frogs co-occur with Yosemite toads (*Bufo canorus*), western toads (*Bufo boreas*; Stebbins, 1985), and long-toed salamanders (*Ambystoma macrodactylum*).

L. Age/Size at Reproductive Maturity. Females reach sexual maturity at 45–50 mm SVL; males mature at a smaller size (Zweifel, 1955). There are few data on age at reproduction, however Zweifel (1955) reports age at first reproduction at 3 yr following metamorphosis. Three or 4 yr after

metamorphosis for high elevation populations seems like a reasonable estimate, but studies of known-age individuals are needed to be certain.

M. Longevity. Unknown.

N. Feeding Behavior. In southern California, mountain yellow-legged frogs prey on a wide variety of invertebrates including beetles (Coleoptera), ants, bees, wasps (Hymenoptera), flies (Diptera), true-bugs (Hemiptera), and dragonflies (Odonata; Long, 1970). This is probably true of Sierran frogs, but there are no reports. Sierran frogs have been observed eating Yosemite toad tadpoles (Mullally, 1953), and Pacific treefrog tadpoles (Pope, 1999). There is one report of Sierran mountain yellow-leg cannibalism—tadpoles eating thousands of conspecific eggs (Vredenburg, in review). In addition, these tadpoles have been seen feeding on carcasses of dead metamorphosed mountain yellow-legged frogs (Vredenburg, in preparation). Pope and Matthews (2002) address the influnce of prey on mountain yellow-legged frog condition and distribution.

O. Predators. Native predators of mountain yellow-legged frogs include western terrestrial garter snakes (*Thamnophis elegans*; Grinnell and Storer, 1924; Mullally and Cunningham, 1956; Jennings et al., 1992), Brewer's blackbirds (*Euphagus cyanocephalus*, in Sierran populations; Bradford, 1991), Clark's nutcrackers (*Nucifraga columbiana*, in Sierran populations; Camp, 1917b), and coyotes (*Canis latrans*; in the Sierra Nevada; Moore, 1929). There are two anecdotal reports of black bears (*Ursus americanus*) feeding on these frogs (Sierran populations; G.M.F., personal communication). Garter snakes in the Sierra Nevada feed extensively on these frogs and commonly are found near large numbers of tadpoles (Jennings et al., 1992). Introduced trout (rainbow trout [*Oncorhynchus mykiss*], golden trout [*O. aguabonita*], brook trout [*Salvelinus fontinalis*], and brown trout [*Salmo trutta*]) have been observed to prey on Sierran mountain yellow-legged frogs (see above; Grinnell and Storer, 1924; Needham and Vestall, 1938; Knapp, 1996).

P. Anti-Predator Mechanisms. When alarmed, adults dive into streams, kick up silt with their hind legs, and bury themselves into the mud (southern California, Camp, 1917b). Similar behaviors have been seen in the Sierra Nevada (Grinnell and Storer, 1924; Wright and Wright, 1933).

Q. Diseases. In a population of Sierran frogs, Bradford (1991) observed a large-scale die-off of frogs that were infected with a bacterium (red-leg disease, *Aeromonas hydrophila*). Recently, a chytridiomycete fungus (likely *Batrachochytrium dendrobatidis*; Longcore et al., 1999) has been identified and cultured from both tadpoles and subadults from the central Sierra Nevada (Fellers et al., 2001). This same chytridiomycete fungus has been implicated in amphibian declines in the rain forests of Australia and Central America (Berger et al., 1998); however, at this time it is not known if this fungus has played a role in the decline of mountain yellow-legged frogs.

R. Parasites. Goodman (1989) described a trematode species from southern California mountain yellow-legged frogs.

4. Conservation. Currently, mountain yellow-legged frogs are found scattered throughout nearly all their historical range in the Sierra Nevada, but the number of populations is greatly reduced. This is most notable in the northernmost 125 km of the range (north of Lake Tahoe) and the southernmost 50 km, where only a few populations have been found in the last few years (Jennings and Hayes, 1994a; G.M.F., in preparation; see "Historical versus Current Distribution" and "Historical versus Current Abundance" above). If we combine the data from the two resurvey studies in the Sierra Nevada (Bradford et al., 1994a; Drost and Fellers, 1996), of the 86 historical sites (data from 1915–'59), only 16 contained frogs when they were revisited between 1989–'95.

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Vance Vredenburg
Museum of Vertebrate Zoology
Department of Integrative Biology
University of California
Berkeley, California 94720
vancev@socrates.berkeley.edu

Gary M. Fellers
Western Ecological Research Center, USGS
Point Reyes National Seashore
Point Reyes, California 94956
gary_fellers@usgs.gov

Carlos Davidson
Environmental Studies Department
California State University
6000 J Street
Sacramento, California 95819-6001
cdavidson@csus.edu