

of such crevices appears to allow them to survive in shallower water bodies that freeze to the bottom in winter (Pope 1999a). In lakes and ponds that do not freeze to the bottom in winter, mountain yellow-legged frogs may overwinter in the shelter of bedrock crevices as a behavioral response to the presence of introduced fishes (V. Vredenburg *et al.* (in press)).

Adult mountain yellow-legged frogs breed in the shallows of ponds or in inlet streams and are often seen on wet substrates within 1 m (3 ft) of the water's edge (Zweifel 1955). Adults emerge from overwintering sites immediately following snowmelt and will move over ice to get to breeding sites (Pope 1999a; V. Vredenburg in litt. 2002). Mountain yellow-legged frogs in the Sierra Nevada deposit their eggs underwater in clusters, which they attach to rocks, gravel, vegetation, or under banks (Wright and Wright 1949; Stebbins 1951; Zweifel 1955; Pope 1999a). Clutch size varies from 15 to 350 eggs per egg mass (Livezey and Wright 1945; V. Vredenburg *et al.* (in press)). In laboratory breeding experiments, egg hatching times ranged from 18 to 21 days at temperatures ranging from 5 to 13.5 Celsius (°C) (41 to 56 Fahrenheit (°F)) (Zweifel 1955). Field observations are similar (Pope 1999a).

The time required to develop from fertilization to metamorphosis is believed to vary between 1 and 4 years (Storer 1925; Wright and Wright 1949; Zweifel 1955; Cory 1962b; V. Vredenburg *et al.* (in press)). Since larvae must overwinter at least two or three times before metamorphosis, successful breeding sites are located in, or connected to, lakes and ponds that do not dry in the summer, and that are sufficiently deep so as to not completely freeze through in winter (Bradford 1983). Larval survival to metamorphosis is possible in lakes that do not dry out during the summer. Knapp and Matthews (2000) found the number of larvae was larger in fishless water bodies deeper than 2 m (6.5 ft). Bradford (1983) found that mountain yellow-legged frog die-offs sometimes result from oxygen depletion during winter in lakes less than 4 m (13 ft) deep. However, larvae may survive for months in nearly anoxic (oxygen-deficient) conditions when shallow lakes are frozen to the bottom. Recent studies have reported populations of mountain yellow-legged frogs overwintering in lakes less than 1.5 m (5 ft) deep that were assumed to have frozen to the bottom, and yet healthy frogs were documented to emerge the following July (Matthews and Pope 1999; Pope 1999a). Radio telemetry indicated that

the mountain yellow-legged frogs were utilizing rock crevices near shore, crevices, holes, and ledges where water depths ranged from 0.2 m (0.7 ft) to 1.5 m (5 ft) (Matthews and Pope 1999). The granite surrounding these overwintering habitats may insulate the mountain yellow-legged frogs from the extreme winter temperatures, providing that there is an adequate supply of oxygen either in the water or air (Matthews and Pope 1999).

Larvae maintain a relatively high body temperature by selecting warmer microhabitats (Bradford 1984). During winter, larvae remain in warmer water below the thermocline (thermally stratified water); after spring overturn (thaw and thermal mixing of the water), they continue to behaviorally modulate their body temperature by daily movements: during the day, larvae move to warm, shallow, nearshore water, and during the late afternoon and evening, they retreat to the warmer waters off shore (Bradford 1984).

The time required to reach reproductive maturity is thought to vary between 3 and 4 years after metamorphosis (Zweifel 1955). Longevity of adults is unknown, but adult survivorship from year to year is very high, so they are undoubtedly long-lived amphibians (Matthews and Pope 1999; Pope 1999a). Although data currently are limited, evidence exists that mountain yellow-legged frogs display strong site fidelity and return to the same overwintering and summer habitats from year to year (Pope 1999a).

In aquatic habitats, mountain yellow-legged frog adults typically move only a few hundred meters (few hundred yards) (Matthews and Pope 1999; Pope 1999a), but distances of up to 1 km (0.62 mi) have been recorded (V. Vredenburg *et al.* (in press)). Adults tend to move between selected breeding, feeding, and overwintering habitats during the course of the year. Though adults are typically found within 1 m (3.3 ft) of water, overland movements of over 65 m (215 ft) have been recorded (Pope 1999a); the furthest reported distance of a mountain yellow-legged frog from water is 400 m (1,300 ft) (V. Vredenburg *et al.* (in press)). Almost no data exist on the dispersal of juvenile mountain yellow-legged frogs away from breeding sites (Bradford 1991). However, juveniles that may be dispersing to permanent water have been observed in small intermittent streams (Bradford 1991). Mountain yellow-legged frog population dynamics are thought to have a metapopulation structure (Bradford *et al.* 1993; Drost and Fellers 1996; Knapp and Matthews 2000). In describing the metapopulation concept, Hanski and

Simberloff (1997) stated: “* * *the two key premises in this approach to population biology are that populations are spatially structured in assemblages of local breeding populations and that migration among the local populations has some effect on local dynamics, including the possibility of population reestablishment following extinction.”

Adult mountain yellow-legged frogs are thought to feed preferentially upon terrestrial insects and adult stages of aquatic insects while on the shore and in shallow water (Bradford 1983). Feeding studies on Sierra Nevada mountain yellow-legged frogs are limited. Remains found inside the stomachs of mountain yellow-legged frogs in southern California include a wide variety of invertebrates, including beetles, ants, bees, wasps, flies, truebugs, and dragonflies (Long 1970). Larger frogs take more aquatic true bugs (insects in the taxonomic order Hemiptera) probably because of their more aquatic behavior (Jennings and Hayes 1994). Adult mountain yellow-legged frogs have been observed eating Yosemite toad (*Bufo canorus*) and Pacific treefrog (*Pseudacris regilla*) larvae (Mullally 1953; Zeiner *et al.* 1988; Pope 1999b; Feldman and Wilkinson 2000) and can be cannibalistic (Heller 1960). Mountain yellow-legged frog larvae graze on benthic detritus, algae, and diatoms along rocky bottoms in streams, lakes, and ponds (Bradford 1983; Zeiner *et al.* 1988). Larvae have also been observed cannibalizing conspecific (of the same species) eggs (Vredenburg 2000). In addition, larvae have been seen feeding on the carcasses of dead metamorphosed frogs (V. Vredenburg *et al.* (in press)).

Status

The distribution of the Sierra Nevada mountain yellow-legged frog is restricted primarily to publicly managed lands at high elevations, including streams, lakes, ponds, and meadow wetlands located on national forests, including wilderness and non-wilderness on the forests, and national parks. Approximately 210 known mountain yellow-legged frog populations (or populations within metapopulations) exist on the national forests within the Sierra Nevada, though not all of these populations may be reproducing successfully. In the national parks of the Sierra Nevada, there are 758 known sites with mountain yellow-legged-frogs, most of which occur within 59 different basins that have multiple breeding populations that are connected hydrologically, so that populations in each basin function as