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In California, overwintering tadpoles have been reported for only two ranid species: *Rana muscosa* (mountain yellow-legged frog) (Stebbins 1985) and *R. catesbeiana* (bullfrog) (Behler and King 1979; Leonard et al. 1993). Storer (1925) states that *R. aurora* spend 4–5 months as larvae with metamorphosis typically taking place between July and September. We report here our observations of *Rana aurora draytonii* (California red-legged frog) tadpoles overwintering at 11 sites spread over four counties in central coastal California. We define overwintering as spending the winter (November–February) in the larval stage (\leq Gosner stage 40; Gosner 1960).

One site is located in a spring-fed pool that drains into Matadero Creek (Santa Clara Co., $37^{\circ}24'$, $122^{\circ}10'$, 200 m elevation). On Mar 20, 1998 we caught two distinct size classes of tadpoles, five small individuals (approximately 30 mm TL), and two large ones (72 mm and 92 mm TL; Gosner stages 36 and 38 respectively). There was also a recently metamorphosed *R. aurora* (28 mm SVL). On Oct 15, 1999 we found a tadpole with only rudimentary hind limbs (Gosner 36). The pool measured 3×5 m and was >1.0 m deep. It was heavily shaded with California blackberry (*Rubus ursinus*), willow (*Salix* sp.), and poison oak (*Toxicodendron diversilobum*).

On Nov 3, 1999 a 65 mm tadpole was caught at one of several pools along a 150 m stretch of Round Valley Creek (Contra Costa Co., $37^{\circ}52'$, $121^{\circ}46'$, 128 m elevation). The tadpole had only small hind limb buds (Gosner 32). On Dec 15, 1999 an additional three tadpoles (Gosner 36–37) were captured in the same creek, and on Jan 7, 2000 one Gosner stage 39 tadpole was found. The creek ran through an oak savannah woodland, which was seasonally grazed by cattle. Two of the pools were >1.0 meter deep including the one where the tadpole was captured. Prior observations indicate that tadpoles have overwintered at this site each year since 1997. Recent metamorphs have been found in April, much too early to be young of that year because eggs are typically laid at this site during March. During winter storms, the creek carries a substantial amount of water and rises as much as a vertical meter, at least for short periods of time. It is not clear how *R. aurora* tadpoles survive these events.

Four ponds in the Kellogg Creek drainage (Contra Costa Co., $37^{\circ}47'$, $121^{\circ}43'$, 323 m elevation) have been observed to have *R. aurora* tadpoles during the late fall and winter for each of the last two years. On Nov 5, 1998, 287 tadpoles were caught at an artificial stock pond located in a heavily-grazed grassland. The tad-

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Overwintering Tadpoles in the California Red-legged Frog (*Rana aurora draytonii*)

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poles ranged in size from 19 to 37 mm SVL, and from 39 to 75 mm TL. None of these tadpoles had hind limbs or hind limb buds (< Gosner 26). Subsequent surveys conducted at this pond demonstrated that tadpoles were present well into the winter (Nov 3, 1999 [3 tadpoles, 83–87 mm, Gosner 38–40]; Feb 8, 2000 [3 tadpoles]; and Feb 12, 2000 [1 tadpole]). Three other ponds in the Kellogg Creek drainage were surveyed in early 1999 (37°48', 121°43', 220–277 m elevation), and overwintering tadpoles were captured on the following dates: Jan 21 (14 tadpoles, < Gosner 37), Feb 12 (9 tadpoles, < Gosner 37), and Mar 3 (12 tadpoles, < Gosner 37). All four of the ponds were located in a heavily-grazed grassland with no trees within 1 km.

On Apr 6, 2000 a pond in Morgan Territory (Contra Costa Co., 37°49', 121°48', 607 m elevation) was surveyed and found to have three overwintering tadpoles (Gosner 45).

On Nov 10, 1999 three tadpoles (72 mm, Gosner stages 34–37) were found in a pond near Abbotts Lagoon (Marin Co., 38°7', 122°56', 24 m elevation). The pond was 75 x 10 m, and > 1.0 m in depth. It was surrounded by introduced Mediterranean grasses, while rushes (*Juncus* sp.), sedges (*Carex* sp.), and marsh pennywort (*Hydrocotyle verticillata*) grew in or near the water.

On Jan 16, 2000 tadpoles were seen at Guadalupe Dunes (San Luis Obispo Co., 34°59', 120°38', 37 m elevation) during a nocturnal survey. Ten overwintering tadpoles were captured that ranged from Gosner stage 25 to 42. All tadpoles appeared to be well nourished and healthy. One additional tadpole (stage 37) was captured at a second, nearby pond on Jan 22, 2000. Both ponds were 35–45 cm deep with water temperature of about 15°C. The shores of both ponds were heavily trampled by cattle, and the aquatic vegetation was browsed. These ponds were located only 400 m from the Pacific Ocean.

Sixteen overwintering tadpoles (Gosner stages 25–40) were found at a second locality in San Luis Obispo County (35°27' 120°55', 10 m elevation) on Jan 23, 2000. These tadpoles were in an arroyo about 1 km southeast of the mouth of Villa Creek, north of Cayucos. All the tadpoles were in a 1 x 2-m plunge-pool that was about 70 cm deep and shaded by a willow tree and two-meter high steep banks. The pool was located about 50 m from the ocean in a heavily-grazed grassland dominated by introduced Mediterranean grasses.

We suspect that overwintering is not common in larval *R. aurora*. We were able to find overwintering *R. aurora* tadpoles at only one of six known breeding sites in Marin County and at only two of seven sites in San Luis Obispo County. California's Mediterranean climate may influence the timing of oviposition (winter) and metamorphosis (summer/fall) in *R. a. draytonii*. High-flow events during winter are normal in California creeks, and undoubtedly provide strong selection pressure for 1) frogs to delay egg-laying, and 2) larvae to complete metamorphosis before winter storms. Eggs laid before March in coastal creeks in San Luis Obispo County have been washed away by late winter storms (GR, pers. obs.). Similarly, tadpoles that do not metamorphose before early winter storms risk being lost. Hence, overwintering in *R. a. draytonii* does not appear to be highly adaptive, especially for populations that breed in streams.

Overwintering in *Rana a. draytonii* is probably closely related to water temperature, an important factor in determining the rate of tadpole development (Altig and McDiarmid 1999). We would

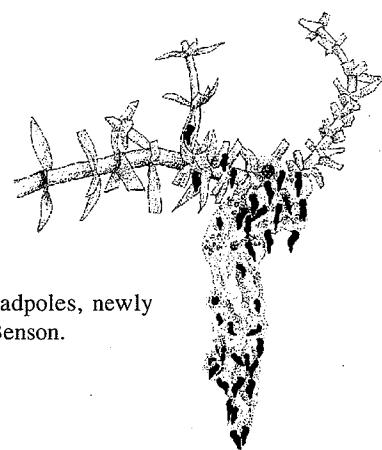
expect to encounter overwintering tadpoles most frequently in high-altitude regions where the warm summer season is short; in aquatic areas with deep shade that prevents solar radiation from warming the water; and along the narrow coastal strip where cold ocean temperatures, prevailing wind, and summer fog create cool summer conditions. Unusually cool summers, as brought about by La Niña ocean cooling, may exacerbate local influences on summer temperatures. *Rana a. draytonii* tadpoles at all the sites described above were living in ponds, pools, or parts of streams that appear to be cooler than is typical for this species. We are currently monitoring temperature at several sites to evaluate whether temperature is likely to be a contributing factor.

Our observations of overwintering *R. a. draytonii* tadpoles are important in part because this frog is Federally-listed and the US Fish and Wildlife Service is in the process of revising guidelines for conducting formal surveys. Our findings indicate that in some areas, surveys for both tadpoles and recent metamorphs may need to be conducted over a much longer period of time since the length of the larval period can range from 4 (Storer 1925) to 13 months (this study).

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Bufo bufo (Common Toad) tadpoles, newly hatched. Illustration by P. A. Benson.