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Further evidence of range-wide overwintering in the larvae of the California red-legged frog *Amerana draytonii* (Baird & Girard, 1852)

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In biphasic amphibians, the larval form of each individual goes through metamorphosis following a larval period that typically lasts between one and three seasons after hatching (Gilbert and Frieden, 1981; Duellman and Trueb, 1994; Dodd, 2013; Petranka, 1998). Some anurans (e.g., *Spea* and *Scaphiopus*) can metamorphose in as little as 7.5 days (Streckler, 1908; Dodd, 2013), while longer-maturing salamanders, such as those in neotenic families (Duellman and Trueb, 1994), remain in the larval form throughout their life. Anuran larvae, however, are not typically neotenic (Gilbert and Frieden, 1981), and the few known cases have been associated with an abnormal thyroid that arrests development (Wassersug, 1975). Some biphasic anurans have larvae that extend development into the second or third season following hatching (Collins, 1979). For example, the American Bullfrog, *Aquarana catesbeiana* (Shaw, 1802), may extend its developmental period into a third year following hatching (Collins, 1979; Bruneau and Magnin, 1980). In California, bullfrogs can also take up to three years to metamorphose (Storer, 1925), but more commonly they metamorphose in one to two years (J. Alvarez, pers obs.). Storer (1925) and Zweifel (1955) reported that the Sierra Nevada Yellow-legged Frog, *Amerana sierrae* (Camp, 1917), a native California ranid, remains a larva for up to two spring seasons following hatching. More recent work may extend that to three seasons for *A. sierrae* (Calatayud et al., 2021).

The closely related California Red-legged Frog, *A. draytonii*, a threatened species in the United States (USFWS, 2002) and a near threatened species on the IUCN Red List (IUCN SSC, 2022), was historically thought to reach metamorphosis in a single season (Storer, 1925). However, overwintering larvae have been observed in several locations (Fellers et al., 2001; Anderson, 2017). Elucidating the frequency and distribution of overwintering in *A. draytonii* is critical because current practices in controlling introduced competitors, such as bullfrogs and introduced fishes, entails manipulating the hydroperiods of waterbodies to inhibit or eliminate introduced species. Such practices would produce collateral effects on overwintering *A. draytonii* larvae. Herein, we report on an additional location of overwintering *A. draytonii* larvae, in the southern extreme of the range (Richmond et al., 2014), indicating a range-wide occurrence of this behaviour.

As part of an ongoing research program monitoring habitat enhancement efforts in habitats historically occupied by *A. draytonii*, we conducted focal animal surveys at Meling Ranch in northern Baja California, Mexico (30.9723°N, 115.7442°W, elevation 640 m). We conducted visual encounter surveys and dip net surveys in both lotic and lentic aquatic habitats, between four and 12 times annually from 2016–2024, during daylight and nighttime hours. When captured, we measured the snout–vent length (SVL) of each frog by hand with a graduated ruler and weighed each frog using a spring scale to the nearest gram. All individuals with SVL > 35 mm SVL were PIT tagged.

The habitat consists primarily of a riparian corridor with a perennial creek system, and five constructed ponds that range from approximately 1–2 m deep and are supplied by groundwater that seeps upward through the sandy pond bottoms. The surrounding uplands are primarily a mix of annual grasslands and chaparral vegetation types. Egg masses were detected at this site from early January–February, which is typical for

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the species (Alvarez et al., 2013a, 2023). During each survey we regularly captured between 50 and 200 post-metamorphic *A. draytonii*. We opportunistically captured 15–20 larvae each year while using dip nets, which were then released. In 2021, we captured eight larvae that appeared to be no less than twice the size of larvae collected in other locations where *A. draytonii* larvae are regularly captured during the same time period (J. Alvarez, pers obs.). In 2022 and 2023 similar observations were made, but little to no effort was expended to determine if additional size cohorts were present. On 3 April 2024 we observed *A. draytonii* larvae foraging and seeking refuge in a pond at Meling Ranch. The larvae appeared to be at Stage 25 or older (Gosner, 1960), and of a size more typically found months later in the season (J. Alvarez, pers. obs.). We captured larval specimens from two distinct size cohorts (Fig. 1A). The same evening, we hand-captured an individual *A. draytonii* larva that had reached a stage of developmental differentiation (Stage 45) penultimate to completing metamorphosis (Fig. 1B).

During our work in 2024, we speculated that the smallest larval size class (Stage 25) we captured (Fig. 1A) likely represented those individuals that hatched in the year of capture (i.e., 2024). This is based on closely monitored captive and wild *A. draytonii* larvae captured during the same time period in other areas. We speculated that the larger larvae (also at Stage 25) likely overwintered at the site. Overwintering larvae may continue to feed and grow in size, but since lower temperatures retard development (Berven et al., 1979), this results in larger but less developed larvae (Fig. 1A). High elevation populations also exhibit continued growth and retarded development (Berven et al., 1979). However, in both cases, overwintering often confers higher fitness to larvae because they enter metamorphosis at a larger size and begin life larger in the saltatory adult form (Wilbur, 1980). Growth rates of larvae are highly variable, and the large size cohort may have exploited more suitable conditions upon which to grow faster. However, at this site, prior to the initiation of annual breeding, thorough egg mass surveys occurred weekly for an ongoing, unrelated project. In addition, water and air temperatures, as well as food resources, are at their lowest during winter, so much so that early breeding and subsequent hatching would likely not benefit from accelerated growth during this period (Duellman and Trueb, 1994).

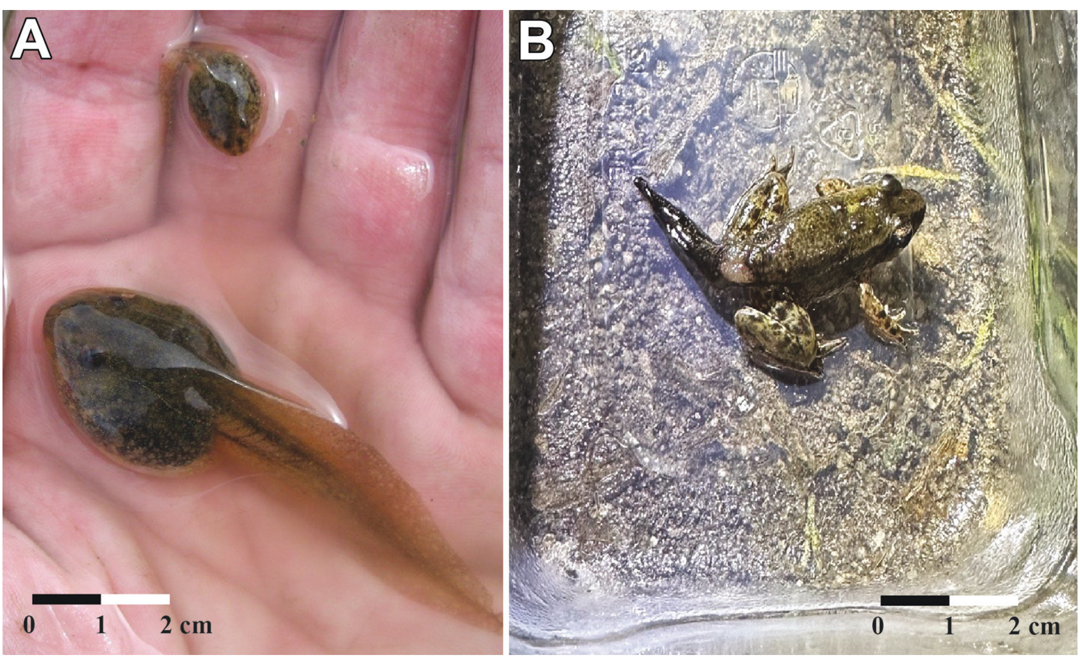

Figure 1. California red-legged frogs (*Amerana draytonii*) captured in Meling Ranch, Baja California, Mexico, in April 2024. (A) Two size cohorts of larval California red-legged frog at Gosner Stage 25. (B) Pre-metamorphic California red-legged frog (at Gosner Stage 45). Photos by Jeff Alvarez.

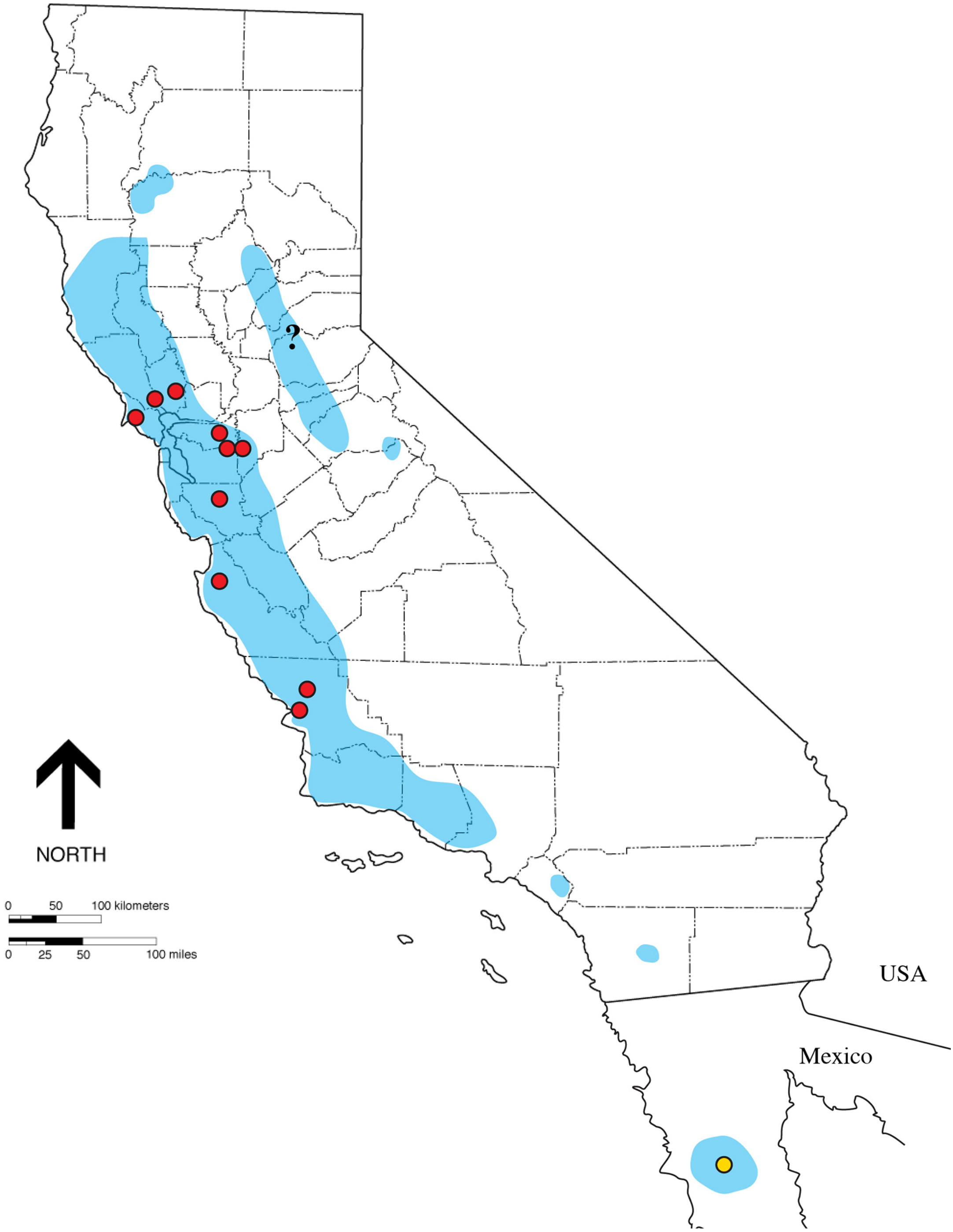

Figure 2. Known locations of overwintering California red-legged frog (*Amerana draytonii*) larvae in California (red dots; Fellers et al., 2001; Anderson 2017; J. Alvarez, pers. obs.) and the newly reported location (yellow dot) in Baja California, Mexico. The question mark indicates likely overwintering at Big Gun Mitigation site, Placer County, CA (J. Alvarez, pers. obs.). Blue shading represents approximate distribution range of the California red-legged frog according to USFWS (2002). Map by Jeff Alvarez.

Therefore, our capture of a pre-metamorphic frog (Stage 45) provides evidence to indicate that some individuals at this site had overwintered as larvae.

Fellers et al. (2001) reported overwintering of 75 larvae of *A. draytonii* at 11 sites in four counties in California, USA, stating that this behaviour was "not common". A later summary of the natural history of the species was contradictory, stating that "overwintering does not occur as larvae" (Dodd, 2013). Subsequent work on overwintering larvae by Anderson (2017) re-interpreted the report by Fellers et al. (2001), stating that the behaviour was "rare". She reported on overwintering of 25 individuals over two years, in a fifth county in California (in addition to four reported by Fellers et al.; Anderson, 2017). We continue to see overwintering behaviour in Contra Costa and Santa Clara Counties, as also reported by Fellers et al. (2001), as well as in adjacent counties (Alameda, San Joaquin, and Sonoma; J. Alvarez, pers. obs.; Fig. 2). We believe that these larvae overwinter in permanent waterbodies regularly, and across a significant portion of the species' range (Fig. 2). Future research should focus on addressing the lack of information from higher elevation populations, such as the Sierra Nevada, California, USA (up to 1100 m) and the Sierra San Pedro Martír (up to 2050 m), Baja California, Mexico. We contend that larval overwintering is highly likely in those populations (i.e., circumstantial evidence at Big Gun, Michigan Bluff, 1070 m), because water temperatures are lower than coastal populations (below 7.5°C; Storer, 1925; Fellers et al., 2001), and growing seasons are shorter. This pattern is consistent with *A. sierrae*, which lives at a similar elevation range and has larvae that regularly overwinter (Zweifel, 1955; Bradford, 1983; Calatayud et al., 2021). We suggest that the phenotypic plasticity of the overwintering trait is likely ubiquitous across the range of the species, regardless of the underlying mechanisms that manifest its expression. This also appears to be true for the closely related congener *A. muscosa* (Camp, 1917), which has putative overwintering larvae throughout their range in California (Zweifel, 1955; Bradford, 1983; Calatayud et al., 2021). This alone indicates that it is more likely to be a range-wide phenomenon rather than isolated individuals that are opportunistically exceeding the typical growth period for the species. Nevertheless, we acknowledge that another closely related congener in California, the Cascades Frog, *A. cascadae* (Salter, 1939), has not yet been reported to overwinter.

Our observations extend the range of overwintering in larval *A. draytonii* to the southern extreme of the range, suggesting that management actions should consider this trait throughout the range of the species. These observations are significant in light of management recommendations from the United States Fish and Wildlife Service (USFWS, 2002) to manually dry down managed ponds to control invasive species. Many authors now recommend that land managers assess the potential presence of overwintering *A. draytonii* larvae before conducting management or habitat enhancement activities at sites where this species may occur (Fellers et al., 2001; Alvarez et al., 2013b; Anderson, 2017). Currently, there is no sufficient larvae monitoring to determine whether draining or drying a water body with *A. draytonii* would impact this declining species. Overwintering is likely an underreported behaviour, and we recommend thorough surveys prior to conducting management actions related to aquatic breeding sites across the range of this species.

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