Syntopy in California red-legged and foothill yellow-legged frogs in their aquatic habitat

December 29, 2023 **RESEARCH NOTE**

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Published 29 December 2023 • doi.org/10.51492/cfwj.109.16

Key words: aquatic, California red-legged frog, declining, foothill yellow-legged frog, management, protected, *Rana boylii*, *Rana draytonii*, range, sympatry, threatened

Citation: Alvarez, J. A., M. Aiken, and J. T. Wilcox. 2023. Syntopy in California red-legged and foothill yellow-legged frogs in their aquatic habitat. California Fish and Wildlife Journal 109:e16.

Editor: Jennifer Olson, Watershed Restoration Grants Branch

Submitted: 13 July 2023; Accepted: 5 September 2023

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Competing Interests: The authors have not declared any competing interests.

Co-occurrence of two or more species of amphibians with biphasic life cycles is extremely common in North America, particularly around the east coast of the United States (Petranka 1998; Lannoo 2005; McGinnis and Stebbins 2018). On the west coast, different amphibians are often sympatric (share the same distribution) and/or syntopic (share the same habitat at the same time) over a wide range of genera and species, including various assemblages of *Ambystoma, Taricha, Dicamptodon, Pseudacris, Spea, Anaxyrus, Rana, Lithobates,* and others (Storer 1925; Petranka 1998; Lannoo 2005; McGinnis and Stebbins 2018; Flaxington 2021). For example, the California giant salamander (*Dicamptodon ensatus*) and northwestern salamander (*Ambystoma gracile*) are commonly found under the same cover objects and often breed in the same aquatic habitats (Storer 1925; Stebbins 2003). The wide-ranging roughskinned newt (*Taricha granulosa*) and California newt (*T. torosa*) are frequently found together in both terrestrial and aquatic breeding habitat where the species are syntopic in the southern portion of the range of *T. granulosa* (Stebbins 2003; Stebbins and McGinnis 2012). Similarly, in Santa Cruz County, the California tiger salamander (*Ambystoma californiense*) and its congener the Santa Cruz long-toed salamander (*A. macrodactylum croceum*) are syntopic (J. Alvarez, pers. obs.). Recently, Alvarez et al. (2013) reported a wide area where the California tiger salamander and California red-legged frog (*Rana draytonii*) were synoptic.

California red-legged frogs are listed as threatened under the federal Endangered Species Act and are an Amphibian Species of Special Concern in California (Thomson et al. 2016). The California red-legged frog is closely associated with aquatic freshwater habitats surrounded by grasslands, chaparral, woodlands, and forest habitat types (Storer 1925; Hayes and Jennings 1988; Bulger et al. 2003; Allaback et al. 2010). The species is frequently syntopic with other native amphibians in their aquatic breeding habitat, including California newt, rough-skinned newt, California tiger salamander, Pacific treefrog (*Hyliola regilla*), western toad (*Anaxyrus boreas*), as well as non-native American bullfrog (*Lithobates catesbeianus*; Storer 1925; Feaver 1971; Hayes and Tennant 1985; Rathbun 1998; Cook and Jennings 2007; Alvarez et al. 2013).

Foothill yellow-legged frogs (*R. boylii*) were a California Amphibian Species of Special Concern since 1994 (Jennings and Hayes 1994), were recently considered candidate species for federal listing (USFWS 2022), and several clades were listed in 2020 under the California Endangered Species Act as threatened or endangered (CFGC 2020). The foothill yellow-legged frog is another Pacific Coast ranid species but is better known for being associated with both perennial and intermittent creeks, rivers, and streams (Zwiefel 1955; Bourque 2008; Bondi et al. 2013; McGinnis and Stebbins 2018). Zwiefel (1955) noted that he rarely found foothill yellow-legged frogs more than a single hop from a creek or stream. More recently Wilcox and Alvarez (2019) and Alvarez and Wilcox (2021a) reported the foothill yellow-legged frogs occasionally use lentic systems for breeding, refuge, and presumably foraging.

The range of California red-legged frogs and foothill yellow legged frogs appear to have intermittent overlapping areas ranging from Mendocino and Plumas counties in the north and extending south into the Sierra Nevada and along coastal California to Baja California in Mexico (**Fig. 1**; Thomson et al. 2016; McGinnis and Stebbins 2018; Flaxington 2021). When declining species are syntopic and also protected by state or federal law, as in the case of these to native ranids, management implications may be considerable. This is particularly true when management activities require actions within aquatic breeding sites for one of the listed species and not the other. If management activities are focused on a single species without regard to the other, the actions may result in changes to habitat suitability or population persistence for one or more life stages, or direct or indirect harm of the untargeted syntopic species (Alvarez et al. 2013). Although the general belief is that the California red-legged frog and foothill yellow-legged frogs would rarely overlap due to niche differentiation (Thomson et al. 2016), we note several locations where the species co-occur and breed, seek refuge, and actively forage in the same location at the same time (i.e., syntopy). We report here numerous accounts of syntopy in the breeding habitat of two protected amphibians that have not been reported elsewhere, which may affect management of both species.



Figure 1. The ranges of California red-legged frog (CRLF), and foothill yellow-legged frog (FYLF), areas of range overlap, and the regions of our sites of investigation in California, 2023. Geographical distributions

of CRLF and FYLF were adapted from Stebbins 2003, McGinnis and Stebbins 2018, and Flaxington 2021. We investigated the occurrence of syntopy in these two species within their ranges in California via both data we collected during our own amphibian surveys and data compiled from recent and historic records. Our observational data were collected during various independent amphibian survey projects over a large area, from spring 2000 to fall 2023 (**Fig. 1**; **Table 1**). Observational data were typically collected during other long-term monitoring efforts that included predator control, amphibian population monitoring, presence/lack of presence surveys, and other survey efforts that focused on aquatic habitat for ranids. Twenty-nine percent of the data were generated from sites where we worked two or more years and where we visited sample sites multiple times. Our surveys were timed such that both species were known to be (or presumed to be, based on previous knowledge of the sites or data from comparable sites) in a detectable life stage. This would also include when neither species was expected to be occupying upland habitats. We typically conducted surveys March through July, when breeding behavior and larval specimens were likely to be associated with aquatic sites, which occurred prior to drying of most ephemeral sites.

Table 1. Location of observed sympatry of foothill yellow-legged frog (*Rana boylii*) and California redlegged frog (*R. draytonii*) in California. Numbers following California Natural Diversity Database (CNDDB) in Source column are occurrence numbers assigned to particular observations.

| Type of Observation | County | Creek/ Watershed | Aquatic Habitat Typeª | Years syntopic [⊳] | Year(s) reported/ observed | Source |
|------------------------|-------------|-----------------------------|-----------------------------|--------------------------------|----------------------------------|--|
| Current | Alameda | Arroyo Mocho | Ephemeral | 3 | 1999, 2002, 2016 | CNDDB (474, 824, 789 |
| Current | Alameda | Upper Alameda Creek | Ephemeral | 2 | 1997, 2014 | pers. obs. |
| Current | Napa | Wragg Creek | Ephemeral | 4 | 2020-2023 | pers. obs. |
| Current | San Joaquin | Corral Hollow Creek | Ephemeral | 2 | 1998, 2014 | pers. obs |
| Current | Santa Clara | Arroyo Hondo | Perennial | 5 | 2005, 2009, 2013-2015 | CNDDB (1336, 1492, 196, 1490) |
| Current | Santa Clara | Coyote Creek | Ephemeral | 1 | 1986, 2017 | pers. obs.; Gonslin 2010 |
| Current | Santa Clara | Llagas Creek | Perennial | 1 | 2016 | CNDDB (169, 1420) |
| Current | Santa Clara | Upper Penitecia Creek | Ephemeral | Inf | 2010 | CNDDB (1337, 410) |

| Type of Observation | County | Creek/ Watershed | Aquatic Habitat Typeª | Years syntopic ^ь | Year(s) reported/ observed | Source |
|------------------------|------------------|---------------------------------|-----------------------------|--------------------------------|----------------------------------|---|
| Current | Sonoma | Carriger Creek | Perennial | 1 | 2002 | pers. obs. |
| Current | Sonoma | Copeland Creek | Ephemeral | 12 | 2002, 2011-2023 | pers. obs.; Alvarez and Wilcox 2021a |
| Current | Sonoma | Turtle Pond ^c | Perennial pond | 1 | 2020 | pers. obs.; Alvarez and Wilcox 2021a |
| Current | Sonoma | Nolan Creek | Perennial | 1 | 2011 | CNDDB (1338, 1474) |
| Current | Sonoma | Mason Creek | Ephemeral | 1 | 2022 | pers. obs. |
| Current | Sonoma | Sheephouse Creek | Perennial | 2 | 2012, 2017 | CNDDB (1828, 1093) |
| Historic ^d | El Dorado | North Fork Cosumnes River | Perennial | inf | 1942 | CNDDB (1923, 1377) |
| Historic | Lake | Putah Creek | Ephemeral | 1 | 1945 | CNDDB (1704, 1706) |
| Historic | Merced | Los Banos Creek | Ephemeral | 1 | 1985 | CNDDB (45, 901) |
| Historic | Monterey | Big Creek | Perennial | 1 | 1975 | CNDDB (5239, 793) |
| Historic | Santa Barbara | Gaviota Creek | Perennial | inf | 1940 | CNDDB (2419, 388) |
| Historic | Santa Barbara | Mono Creek | Ephemeral | 1 | 1940 | CNDDB (2418, 1509) |
| Historic | Santa Barbara | Refugio Creek | Ephemeral | inf | 1976 | CNDDB (819, 938) |
| Historic | Santa Clara | East Fork Coyote Creek | Ephemeral | 1 | 2004 | CNDDB (420, 798) |

| Type of Observation | County | Creek/ Watershed | Aquatic Habitat Typeª | Years syntopic [⊾] | Year(s) reported/ observed | Source |
|------------------------|--------------------|-----------------------------|-----------------------------|--------------------------------|----------------------------------|--------------------------|
| Historic | Santa Clara | Guadalupe Creek | Ephemeral | 1 | 2000 | CNDDB (736, 420) |
| Historic | Santa Clara | Grizzly Gulch | Perennial | 1 | 2004 | CNDDB (419, 792) |
| Historic | Santa Clara | Middle Fork Coyote Creek | Ephemeral | inf | 1986 | CNDDB (199, 1545) |
| Historic | Santa Clara | Smith Creek | Perennial | 2 | 1950, 1975 | CNDDB (56, 1547) |
| Historic | Santa Clara | Soquel Creek | Perennial | 1 | 2004 | CNDDB (79, 788) |
| Historic | Santa Clara | Stanford University | Perennial | 1 | 1896 | CNDDB (2083, 1551) |
| Historic | Tuolumne | Woods Creek | Perennial | 1 | 1950 | CNDDB (1955, 571) |
| Historic | Baja California | Woods Creek | Perennial | 1 | 1961 | Loomis 1965 |

^a Habitat type at the location of observation

^bYears syntopic is the numbers of reported or observed years species were found together; "inf" is inferred syntopy due to being present at the same site within three years of reported observations.

^c Artificial water body

^d Observation categorized as historic (i.e., prior to the year 2009)

We sampled both lentic and lotic habitats with a wide range of water bodies that included physical characteristics such as: perennial and ephemeral; natural and constructed; turbid to clear waters, small and large (0.004–9.8 ha); deep and shallow (0.2–10 m); low to high elevation sites (10–2070 m); sites nested within grasslands, woodlands, and chaparral; water bodies that were contained within grazed and ungrazed lands, and those supporting a range of emergent vegetation present (0–75% cover), as well as other characteristics. Our reported observations included all aquatic sites within our access area, without regard to a subjective standard for suitability. In most cases, investigators used seines and hand-held dip nets to capture larvae; occasionally post-metamorphic and adult individuals were detected visually during site visits.

In addition to our own personal observations, we conducted a search using the California Natural Diversity Database (CNDDB) of sites that were reported as occupied by these species. Our criteria required that both species be present within a three-year period. Although both species appear to be long-lived (i.e., 15 years for both California red-legged frog [Peralta-Garcia et al. 2022] and foothill yellow-legged frog [J. Drennan, Wildlife Biologist, Kleinfelder, pers. comm.]), we used 3 years since that appeared to be the approximate average of all reported ages for both species to reach breeding age (capable of being detected at any life stage). We then categorized sites with observations older than 15 years (the presumed approximate lifespan of either species) as historic (n = 16) and those before 2008 as contemporary (n = 14). We acknowledge that using a three-year span of time requires us to infer syntopy; however, we included only five sites that required this inference. These sites were included due to our personal knowledge of the long-term presence of both species in these watersheds but where few reported observations exist. We also acknowledge personal knowledge of extant available and appropriate habitat at these sites. All other sites included contemporaneous occurrence of both species from 1 to 12 years (mean = 1.93 yrs).

Our own field research produced six locations where we directly identified both species co-occurring at a site between 2 and 12 years (Table 1). Foothill yellow-legged frogs were detected in one stock pond (i.e., Turtle Pond, Mitsui Ranch, Sonoma County) and were syntopic with a large population of California redlegged frogs using the pond (Alvarez and Wilcox 2021a). Foothill yellow-legged frogs were also observed in several creeks that are typically intermittent or ephemeral. In other areas, such as Copeland Creek in Sonoma County, both species were regularly present at the same site in the same pools, at the same time period (Erway 2022; Wilcox, unpublished data). This frequency of co-occurrence is similar in Napa County at Wragg Creek where a large pool (20 m x 20 m x 2 m deep) was occupied by both species when the pool was full. When the same pool dried, presumably both species occupied similar upland habitat for refuge sites adjacent to the creek (pers. obs.). We visited a site in Baja California at an elevation of 2,075 m where Loomis (1965) reported collecting two foothill-yellow legged frogs. At the time of our visit (58 years later), the habitat appeared as described by Loomis but only California red-legged frogs were present and were abundant. Further, Welsh (1988) also reported no indication of foothill yellow-legged frogs in this area and considered them marginal species in this region. Our visits suggest that habitat is present, but we were not able to conduct night surveys which would have elucidated presence or lack of presence more clearly (Alvarez and Wilcox, in press).

We found six contemporary observations that were reported through the CNDDB that were syntopic (**Table 1**). An additional 16 sites were considered historic (reported >15 years ago), with habitat that appears to remain intact and therefore may potentially support both species currently. We also had eight additional personal observations of sites that were contemporary, which totals 14 separate recent sites from five counties where the species can be found at the same site, in the same habitat, and at the same time (**Table 1**). Although our contemporary data are lacking observations in the Sierra Nevada, Barry and Fellers (2013) suggested that California red-legged frogs and foothill yellow-legged frogs were possibly syntopic in the Sierra Nevada. However, little work has been done in the Sierra Nevada largely due to immense private property ownership where the two species' ranges overlap.

In our compiled data, it was uncommon to detect both species in the same water body but enough to prompt us to investigate whether this is a common occurrence over a larger geographic area (i.e., multiple counties or hydrologic units). We suggest that where these species are sympatric, they are occasionally syntopic. Since the California red-legged frog is an anuran-eating species (Hayes and Tennant 1985; Alvarez 2013), and foothill yellow-legged frogs are a significantly smaller species, especially in the post-metamorphic stage, this may pose a threat to the foothill yellow-legged frogs (McGinnis and Stebbins 2018; Alvarez et al. 2022). However, in a recent study where the two species are syntopic in Copeland Creek, Sonoma County, Erway (2022) reported that niche separation may be driven by frog size. Smaller frogs of both species remain close the wetted edge of the creek pools, while large adult California red-legged frogs are able to bask and forage further from the wetted edge because their

surface-to-volume ratio allows them to thermoregulate more efficiently, therefore maintaining better hydration away from the water.

Although detected in stock ponds (Wilcox and Alvarez 2019; Alvarez and Wilcox 2021a), we recognize that these species did not naturally occur in ponds to the extent that we see them today because natural ponds were uncommon prior to European settlement (Schoenherr 1976). Thus, California red-legged frogs certainly evolved in lotic systems, and these were likely ephemeral systems that had intermittent pools that were suitable for oviposition and larval development. Since both species evolved in and were adapted for lotic habitats, it is reasonable to think both species historically overlapped in these systems.

Management concerns such as managed hydroperiod, extent of emergent or riparian vegetation, presence of potential predators, or breeding frequency may also vary between the two species. Nonetheless, our observations suggest that aquatic breeding habitat that is preserved, restored, or created within the range of both species—although frequently developed and managed for only one species—may well be used by both. This might include re-vegetating the margins or recontouring slopes adjacent to lotic habitats for restoration that may ultimately alter suitability for one or more species (Alvarez and Wilcox 2021b). The habitat requirements of both species should be carefully considered when developing or managing aquatic breeding sites, particularly low gradient streams within the overlapping range of these amphibians.

Our data indicate a pattern of syntopy among these two declining ranids within various aquatic habitats and over a large area—five counties currently with five additional counties historically—within their overlapping geographic ranges. Additional studies may further validate and expand the pattern we observed here.

Acknowledgments

We gratefully acknowledge The Sonoma Mountain Ranch Preservation Foundation, The Land Trust of Napa County, The East Bay Regional Park District, and California State Parks, for access to sites they manage. Joe Drennan of Kleinfelder generously shared information on the lifespan of foothill yellowlegged frogs. The Sonoma Mountain Ranch Preservation Foundation, The Wildlife Project, and Becky Rozumowicz-Kodsunit at Area West Environmental, Inc, supported this project in numerous ways and added to its success. We are also grateful to two anonymous reviewers who thoroughly reviewed an early draft of the manuscript and added greatly to its readability and clarity.

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