Title

HOMECOMING OR NEW PAD: HISTORICAL EVIDENCE FOR CALIFORNIA RED-LEGGED FROGS AND OTHER AMPHIBIANS IN THE YOSEMITE REGION, CALIFORNIA

Journal

Northwestern Naturalist, 104(1)

ISSN

1051-1733

Authors

Adams, Andrea J
Brown, Kevin C
Jennings, Mark R
et al.

Publication Date

2023-02-23

DOI

10.1898/NWN21-04

Peer reviewed

HOMECOMING OR NEW PAD: HISTORICAL EVIDENCE FOR CALIFORNIA RED-LEGGED FROGS AND OTHER AMPHIBIANS IN THE YOSEMITE REGION, CALIFORNIA

ANDREA J ADAMS

Resources Management and Science Division, Yosemite National Park, 5083 Foresta Road, El Portal, CA 95318 USA;
Earth Research Institute, University of California, Santa Barbara, 6832 Ellison Hall, Santa Barbara, CA 93106 USA; andrea_adams@ucsb.edu

KEVIN C BROWN

Environmental Studies Program, University of California, Santa Barbara, 4312 Bren Hall, Santa Barbara, CA 93106 USA

MARK R JENNINGS

Rana Resources, PO Box 2185, Davis, CA 95617 USA; Research Associate, Department of Herpetology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118 USA

ROBERT L GRASSO

Resources Management and Science Division, Yosemite National Park, 5083 Foresta Road, El Portal, CA 95318 USA

ABSTRACT—Establishing historical species distributions can assist conservation translocations for threatened species, and yet, ecological changes necessitate developing restoration targets that are not analogous to historical baselines. Despite its recent conservation translocation to Yosemite Valley in Yosemite National Park, Sierra Nevada Mountains, USA, the historical distribution of the federally threatened California Red-legged Frog (*Rana draytonii*) in the valley remains unclear. Using archival records, interviews, and museum specimens, we examined the historical evidence for California Red-legged Frogs and sympatric amphibian species in the Yosemite region. We found a paucity of reliable amphibian records for Yosemite Valley since the 19th century, one of the most-visited sites in the US National Park System, and conclude that this is the result of historically low collecting and survey effort prior to the introduction of invasive American Bullfrogs (*Lithobates catesbeianus*; also *Rana catesbeiana* after Yuan and others 2016) in concert with a bird and mammal study bias from largely diurnal collecting that occurred when California Red-legged Frogs were extant regionally. We found previously undocumented records for individuals of the genus *Rana* for Yosemite Valley, consistent with a dominant historical hydrology more compatible for Foothill Yellow-legged Frogs (*Rana boylii*), though none could be definitively identified as California Red-legged Frogs. We conclude that extensive anthropogenic impacts, including acute ecosystem alteration and American Bullfrog introduction, contributed to the failure to detect California Red-legged Frogs in many places regionally once amphibians became a research priority in the latter 20th century. The conservation translocation of California Red-legged Frogs to Yosemite Valley illustrates the integration of historical baselines with contemporary realities, allowing for the complexities of change over time rather than focusing on restoration to an imagined, ideal environment in the past.

Key words: amphibian declines, *Anaxyrus boreas halophilus*, endangered species, historical ecology, *Hyla regilla*, *Lithobates catesbeianus*, *Pseudacris regilla*, *Rana draytonii*, novel ecosystems, reintroductions, rewilding, Yosemite Valley

Conservation translocation is becoming an increasingly used management tool to address unprecedented biodiversity losses. Such efforts are complex and challenging, however, leading to low rates of success (Wolf and others 1998; Germano and others 2014). Decisions to translocate threatened and endangered species are frequently based on known historical distributions, and historical records can inform targets for species' recovery (Rodrigues and others 2019). At the same time, rapidly changing ecosystems can diminish the relevance of baseline data, highlighting their context-dependent value and influencing the likelihood of translocation success (Forbes and others 2020).

Anthropogenic stressors—from habitat alteration to invasive pathogens—threaten amphibian populations globally (Cushman 2006; Becker and others 2007; Collins 2010; Adams and others 2017a). Conservation translocations are increasingly employed as one approach to ameliorate amphibian declines (Harding and others 2016). We broadly define conservation translocations as the release of individuals for the purpose of reestablishing extirpated populations, augmenting existing ones, or establishing new populations where either a species' historical status is unknown or the species was not present (Seddon 2010; IUCN 2013).

The federally threatened California Red-legged Frog (*Rana draytonii*) was first translocated to Yosemite Valley (Valley), in Yosemite National Park (Yosemite), in 2016. In the Valley, suitable California Red-legged Frog habitat is present in quiet backwater areas and large, seasonally-flooded wet meadows within the Merced River floodplain (US National Park Service 2000a) providing a safe harbor for the species that is free of its most ubiquitous threats, such as urbanization, agriculture, and invasive species (US Fish and Wildlife Service 2022). Despite the current presence of suitable habitat, the historical occupancy of California Red-legged Frogs in the Valley and in the greater Yosemite region remains unclear.

Ecosystems are dynamic and knowledge of their past conditions is often imperfect; therefore, the use of many different types of historical sources—such as interviews, specimens, letters, and field notes—is more likely to produce the most accurate model for establishment of historical baselines (Swetnam and others 1999). Here, we examined multiple lines of evidence for California Red-legged Frog historical distribution in Yosemite Valley and vicinity. We aimed to address the following questions: (1) what evidence is there for the historical distribution of California Red-legged Frogs in Yosemite Valley prior to its introduction in 2016; (2) what evidence is there for other amphibians on the Yosemite Valley floor (in order to infer relative effort in amphibian surveys and collection); (3) is the relative paucity of amphibian records for Yosemite Valley and vicinity true evidence of absence or simply absence of evidence; and (4) if the latter, what are the reasons for limited collecting and observations in one of the most-visited natural landscapes in the world?

Methods

We used archival records, interviews with experts, and museum specimens to comprehensively examine the evidence for California Red-legged Frogs and other sympatric amphibians in the study area. We compiled occurrence records for ranid species and evaluated their reliability following a method for inferring species' distributions. Additionally, we assessed potential reasons for the paucity of reliable records in the study area.

Study Area

Yosemite National Park encompasses a 3027 km^2 landscape within the Sierra Nevada Mountains of California, a biogeographically significant feature of North America and the tallest mountain range (4421 m) in the conterminous United States. In the Sierra Nevada, amphibian declines have been reported since the 1960s (Moyle 1973; Bradford 1991; Drost and Fellers 1996; Jennings 1996; Hayes and others 2016; Brown and others 2019; Sadinski and others 2020). These reports have rendered the region nearly synonymous with amphibian declines, and therefore a model location for conducting feasibility studies for amphibian conservation translocations (Brown and others 2021; Keung and others 2021).

The approximately 15 km^2 Yosemite Valley (elevation = 900–1280 m) is on the western slope of the Sierra Nevada, and the Merced River meanders on the Valley floor. Historically, the Valley was extensively impacted by prevailing management strategies of different eras (Greene 1987; Hobbs and others 2006), while some efforts

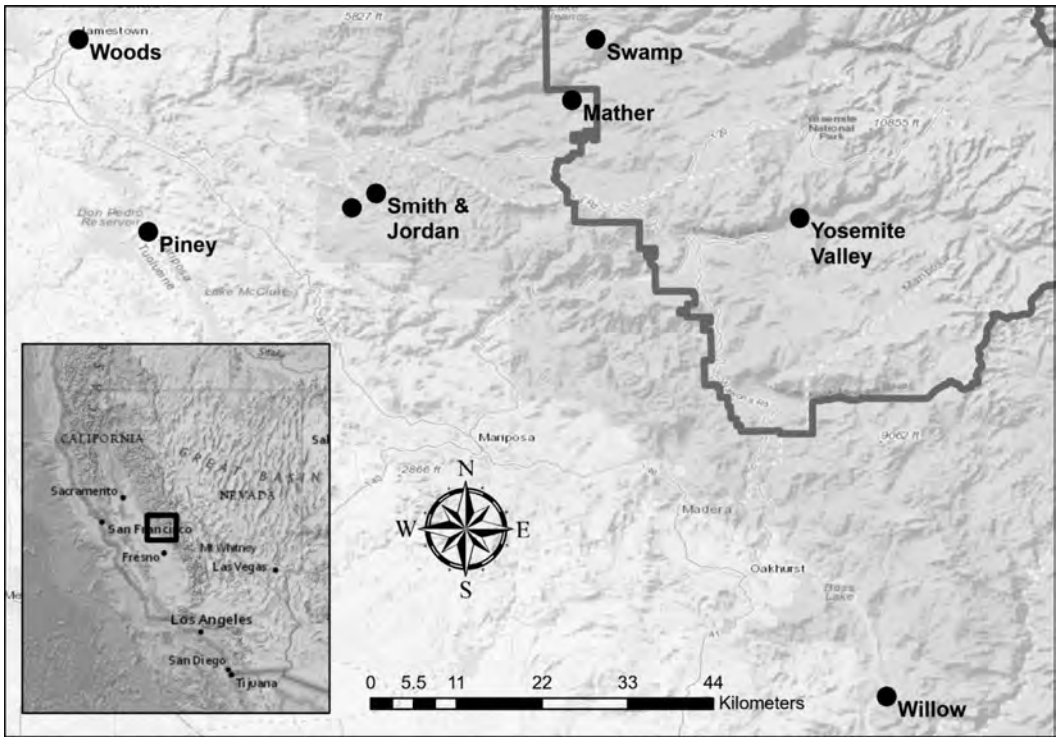

FIGURE 1. California Red-legged Frog (*Rana draytonii*) localities in the study area. The gray line demarcates the Yosemite National Park boundary.

were made to document the biodiversity of the region (Hall 1921; Grinnell and Storer 1924; Wright and others 1933; Moritz and others 2011).

For the purposes of our records search for California Red-legged Frogs, we included 7 historically occupied California Red-legged Frog sites outside of, but in close proximity to the Valley, including: Camp Mather, Swamp Lake, and Jordan, Smith, Piney, Woods, and Willow Creeks (Fig. 1). Camp Mather (Birch Lake [also known as Hog Ranch]; 1378 m elevation; 28 km northwest of the Valley, Tuolumne County) is a recreational area owned and maintained by the City of San Francisco, which is surrounded by the Stanislaus National Forest, and immediately adjacent to the Mather Ranger Station just within the Yosemite National Park boundary. The Miguel Meadow Complex region includes Gravel Pit and Swamp Lakes in Yosemite National Park (1537 m elevation; 32 km northwest of the Valley; Tuolumne County). The Swamp Lake Research Reserve was established as a long-term natural study site in the 1930s because of its lack of systematic specimen collections, its public inaccessibility by motorized vehicle, and its unique biological complexity (Grinnell and Storer 1924; Yosemite Field School 1938). Outside of Yosemite National Park, we included Jordan (808 m elevation; 43 km west of the Valley), Smith (910 m elevation; 45 km west of the Valley), and Piney Creeks (336 m elevation; 62 km west of the Valley) in Mariposa County, Willow Creek (400 m elevation; 70 km south of the Valley) in Madera County, and Woods Creek (560 m elevation; 85 km northwest of the Valley) in Tuolumne County (Fig. 1).

Study Species

California Red-legged Frogs were listed as threatened under the US Endangered Species Act due largely to its >70% decline within its range (US Fish and Wildlife Service 1996), resulting from overharvest, habitat loss, nonnative predators and competitors, and potentially exposure to pesticides and an invasive pathogen (Jennings and Hayes 1994; Davidson and others 2001; US Fish and Wildlife Service 2002; Russell

and others 2019). The fungal pathogen *Batrachochytrium dendrobatidis* (Chytrid), the causative agent of the often-lethal disease chytridiomycosis (Longcore and others 1999), may have contributed to the California Red-legged Frog's decline. At a Sierra Nevada site, 1 juvenile individual succumbed to chytridiomycosis (Adams and others 2020), and chytridiomycosis mortality has been observed in adults in southern California (Adams 2022). Lower survivorship has also been observed in California Red-legged Frog populations with higher Chytrid prevalence (Russell and others 2019). California Red-legged Frogs, which were experimentally infected with and cleared of the fungus, were released to the Valley and subsequently contracted infections (Adams and others 2022).

California Red-legged Frogs formerly occurred throughout much of California, including the foothills of the Sierra Nevada (Jennings and Hayes 1994; Jennings 1996), and currently occur from Mendocino County to the north (Shaffer and others 2004), to northern Baja California, México to the south (Peralta-Garcia and others 2016). Once abundant in many parts of California, the species experienced severe declines in the 1850s during the California Gold Rush, when frog legs were popular cuisine (Jennings and Hayes 1985). By the early 20th century, the California Red-legged Frog was considered a "sparse resident" on the western slope of the Sierra Nevada (Grinnell and Storer 1924), and is even more sparsely distributed a century later (Davidson and others 2001; Barry and Fellers 2013). Reviews by herpetologists of specimen-derived evidence, combined with contemporary resurveys of suitable habitats, have led to the conclusion that California Red-legged Frogs were never widespread in the Yosemite region, and that high elevation populations (>1100 m; including all Yosemite localities) may have been introduced in the early 20th century as a food resource (Barry and Fellers 2013). Assessing occurrences of California Red-legged Frogs in the Yosemite region has proven difficult, owing in part to the species' cryptic, nocturnal habits (Storer 1925; Barry and Fellers 2013).

The Foothill Yellow-legged Frog (*Rana boylii*) is a stream obligate generally known to occur at higher elevations (0–1940 m) than the California Red-legged Frog (0–1500 m) (Jennings and Hayes 1994). The Foothill Yellow-legged Frog has declined from 54% of its former range due to habitat alteration, pesticides, invasive predators and competitors, and disease (Moyle 1973; Jennings 1995; Kupferberg 1997; Davidson 2004; Adams and others 2017a, 2017b).

Introduced from the eastern USA, American Bullfrogs (*Lithobates catesbeianus*; also *Rana catesbeiana* after Yuan and others 2016; hereafter "Bullfrogs") have been implicated in the severe declines of native anurans in California and elsewhere in western North America (Moyle 1973; Hayes and Jennings 1986; Kupferberg 1997; Kiesecker and Semlitsch 2003; Pearl and others 2004). Bullfrogs were first recorded in California in 1896 (Heard 1904; Storer 1933), and later invaded the Sierra Nevada foothills after the species was widely introduced in nearby lowland riparian habitats during the 1920s and 1930s (Storer 1933; Moyle 1973). The earliest known Bullfrog translocations to the Sierra Nevada occurred in 1918 (Jennings and Hayes 1985; Basey 1991). Once Bullfrogs arrive at a site, California Red-legged Frogs often disappear or the population experiences a precipitous decline (Hayes and Jennings 1986), and the species' abundance has been shown to be negatively correlated with the presence of Bullfrogs (Fisher and Shaffer 1996; Lawler and others 1999). When sympatry is present, it is usually the result of niche partitioning or indicative of an early Bullfrog invasion.

In order to more completely assess overall historical amphibian survey effort, we examined the occurrences of 3 additional amphibian species due to shared habitat or frequent sympatry with the California Red-legged Frog: the Pacific Chorus Frog (*Pseudacris regilla*; hereafter "Chorus Frog"); the California Toad (*Anaxyrus boreas halophilus*); and the Sierran Newt (*Taricha sierrae*). To clarify species names: (1) *P. regilla* was split into 3 species, with the portion of the range that includes Yosemite renamed as *P. sierra* (Sierran Chorus Frog; Recuero and others 2006a,b); and (2) *Taricha torosa* was split into 2 subspecies by Riemer (1956), and into 2 species (*T. torosa* and *T. sierrae*) by Kuchta (2007). We consider *T. torosa* specimens and records in the study area to be *T. sierrae* based on this nomenclature change and the phylogeography of the species (Kuchta 2007).

Records Searches

We researched historical occurrence records for amphibians in the Valley using museum specimens, literature review, and accounts of observers, in addition to indirect evidence, including personal papers, interviews, field notes, and US National Park Service memos. We used the primary interviews, field notes, correspondence, and questionnaires collected during a status review of amphibians and reptiles in California (Jennings and Hayes 1994), including statements from many now-deceased individuals with 1st-hand field experiences during the mid-20th century. We conducted keyword searches for subject, geography, and species (i.e., "frog", "red-legged", "bullfrog", "Yosemite", "Yosemite + frog", "Yosemite Valley") using: Biodiversity Heritage Library (https://www.biodiversitylibrary.org); Yosemite Nature Notes (pre-1961; http://www.yosemite.ca.us/library/yosemite_nature_notes); JSTOR (https://www.jstor.org); Chronicling America (https://chroniclingamerica.loc.gov); Google Books (https://books.google.com); HathiTrust (https://www.hathitrust.org); and Search Yosemite Online (http://www.yosemite.ca.us/search.html). We searched the John Muir Papers using: University of the Pacific Scholarly Commons (https://scholarlycommons.pacific.edu); Bade and Muir's 1924 The Life and Letters of John Muir (https://vault.sierraclub.org/john_muir_exhibit/ life/life_and_letters); and Sierra Club Bulletin (online records 1893–1924; https://www. sierraclub.org/library/sierra-club-bulletin). We used the Online Archive of California (https://oac.cdlib.org) to examine finding aids (individual collection metadata) for the Yosemite Archive collections and used them to identify collections with amphibian information, which were subsequently examined at the Yosemite Archives. We used the Museum of Vertebrate Zoology Ecoreader (http://ecoreader.berkeley.edu) to examine field notes from naturalists and collectors.

We used the VertNet museum records database (http://vertnet.org) and the California Natural Diversity Database (https://wildlife.ca.gov/Data/CNDDB) to search for locality and specimen records. We also searched the Natural History Museum of the United Kingdom (https://www.nhm.ac.uk). To determine the relative collecting effort for anuran species in the Valley, we searched for all variations of relevant species names (*Pseudacris regilla*; *Pseudacris sierra*; *Hyla regilla*; *Rana catesbeiana*; *Rana boylii*; *Rana boylii boylii*; *Rana boylii sierrae*; *Rana sierrae*; *Rana draytonii*; *Rana aurora*; *Rana aurora draytonii*; *Lithobates catesbeianus*; *Lithobates catesbeiana* (sic); *Anaxyrus boreas halophilus*; *Anaxyrus boreas*; *Bufo boreas*; *Triturus torosus*; *Taricha torosa*; *Taricha sierrae*) and alternately for the locality "Yosemite" and the county "Mariposa". We limited our Yosemite Valley searches to collecting years 1800–1965, since the latter date is 10 y past the 1st record of Bullfrogs in the Valley (Richards 1958). We examined all ranid specimens in the Yosemite Museum collection to confirm accuracy of species identifications and accession records, and to compare these with field notes and other records obtained during archival research (Jennings 1988; Barry and Fellers 2013; Santana-Cordero and Szabó 2019).

Anecdotal information can be valuable for determining historical or extant ranges of rare or elusive species; however, these data are vulnerable to omission or commission errors. The establishment of *a priori* evidentiary standards allows for the use of anecdotal information while simultaneously ranking the data on the basis of reliability (McKelvey and others 2008). We developed evidentiary standards, adapted from Frey (2006), McKelvey and others (2008), and Garwood and others (2013), for the reliability of ranid records in the Yosemite region as follows: 1 = expert evaluation of either a preserved ranid specimen with diagnostic species-specific characteristics or of a suitable contemporary photograph of a living ranid frog; 2 = 1st-hand observation by an expert; 3 = 2nd-hand report by an experienced observer from an experienced observer; 4 = 1st-hand observation by a less-experienced observer; 5 = 2nd-hand report by an inexperienced observer; 6 = any report with inadequate or questionable identification or locality data. We then grouped these categories as reliable (levels 1–3) or unreliable (levels 4–6).

Results and Discussion

We uncovered 14 new records representing a minimum of 33 individuals of the genus *Rana* in the study area. Five records and 22 individuals were California Red-legged Frogs (Appendix Table 1). None of the records from Yosemite Valley could be definitively identified as Cal-

ifornia Red-legged Frogs. Moreover, we found a paucity of records for amphibians in the Valley, despite its frequent visitation. Finally, Bullfrog introduction, extensive habitat alteration, de-emphasis of amphibians and reptiles by visiting and resident naturalists, lack of nocturnal surveys, and park administrative priorities toward fish and game species and away from non-game wildlife, all contributed to the lack of reliable records of native amphibians in the study area during the time period of interest.

History of Anurans in the Study Area

Pre-contact to late 19th century.—Radio carbon dating and archaeological evidence indicate that humans have occupied Yosemite Valley since at least 5200 y before the present (Moratto and others 1999; Gassaway 2009), and possibly earlier. In adjacent low-elevation zones, there is evidence of human use up to 9000 y ago; in addition, some tribal members may claim their ancestors have lived in the area forever (W Willis, Yosemite National Park, pers. comm.). Yosemite Valley is part of the ancestral territory of the Southern Sierra Miwok tribe. There is clear evidence that both Miwok and Paiute groups occupied the Valley in the contact era and historic period, with less evidence of Yokut visits to the area (Bennyhoff 1956; Gassaway 2009; W Willis, pers. comm.). Descendant populations are commonly grouped into Miwok, Paiute, and Mono groups, each of which have used Yosemite Valley, and 7 tribes are traditionally associated with Yosemite National Park (W Willis, pers. comm.).

A glossary of Southern Sierra Miwok language (Barrett 1919) includes separate words for "frog" and "bullfrog", which would have been translated into English by settler-colonizers of European origin, most likely from the eastern USA. The 2 names for different frogs suggest differentiation between large frogs (of the genus *Rana*; either Foothill Yellow-legged Frogs or California Red-legged Frogs in Yosemite Valley; or Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) in the higher elevations of the Sierra Nevada); and a more diminutive frog, the wider-ranging, more ubiquitous Chorus Frog. "Bullfrog" was a general term commonly used for large frogs by settler-colonizers. This is exemplified in the Sierra Nevada by the naming of Bullfrog Lake in what is now Sequoia-Kings Canyon National Park, although this lake was never occupied by American Bullfrogs; however, it was once inhabited by the Sierra Nevada Yellow-legged Frog prior to the introduction of non-native fish and Chytrid.

The Ahwahneechee people were first forced out of the Valley in 1851 by the Mariposa Battalion militia, less than 20 y before the 1864 Yosemite Grant, which ceded the Valley to the State of California as a park (Sanford 2019). In 1890, the Yosemite Act made human settlements illegal, which ultimately resulted in the removal of most of the Ahwahneechee from the Valley (US Congress 1890; Dowie 2009). John Muir and the naturalists that followed in the late 19th and early 20th centuries commonly disparaged and denigrated indigenous uses and knowledge of nature (Dowie 2009), leaving the natural history literature devoid of investigations or inclusion of traditional ecological knowledge (Inglis 1993). Native voices and perspectives were therefore largely omitted from the founding of natural history as a discipline, and the results of our research reflect this disparity.

In this early settler-colonizer period, Muir journaled and wrote extensively of his experiences in the Yosemite region during the latter part of the 19th century (Badè and Muir 1924), and we uncovered 60 instances in which the word "frog" was mentioned in his writings from that time. Muir frequently mentions the frog chorus; this was presumably a Chorus Frog, owing to its distinctive call (Storer 1925). He also refers to the frog as "Hyla", which is the former genus name for this species (Hedges 1986; Recuero and others 2006b).

Two Muir writings provided evidence that there was a ranid frog species historically present in Yosemite Valley. The first strongly suggests that he encountered ranids in his cabin near the base of Yosemite Falls, where he dug a small ditch from Yosemite Creek so that a portion of the stream would flow into the cabin. Ferns grew up through the rough slabs of the floorboards, attracting aquatic wildlife: "Dainty little tree frogs occasionally climbed the ferns and made fine music in the night, and common frogs came in with the stream and helped to sing with the Hylas and the warbling, tinkling water" (Muir 1869; Appendix Table 1).

Muir referred to the frog other than the *Hyla* as a "Common Frog". The Common Frog, *Rana temporaria*, is widespread in western Europe,

including Scotland (Amphibiaweb 2020), where Muir lived until the age of 11, and which left a strong impression on him, as indicated by the extent of his reflections on the place in his autobiography (Badè and Muir 1924). This suggests that Muir encountered a ranid in Yosemite Creek at his cabin (Appendix Table 1). The Common Frog (*Rana temporaria*) is small (50–110-mm adult length; Halliday 2015), so Muir could have been observing a large Foothill Yellow-legged Frog (38–81-mm adult length) or a smaller California Red-legged Frog (44–133-mm adult length; Stebbins 2003). Contemporary with Muir, Coombes (1902) refers to a "common edible frog" of the San Francisco area, with natural history characteristics (for example, the need for emergent vegetation for oviposition) that associates the name "common frog" with the California Red-legged Frog (Jennings and Hayes 1985).

Muir (1874) refers to "two small frogs of a new species each snuggled in a dainty [illegible] from which they could look out over the water..." that he discovered in a vertical portion of the river bank while swimming in Yosemite Valley (Appendix Table 1). He captured the frogs to take them back to his room in hopes that they "may sing like crickets or tree frogs for me in the night." Muir therefore knew this frog species to be one other than the Chorus Frog. Archivists have not been able to discern the illegible word from the letter, but the context suggests a type of hole or cavity. Such behavior is characteristic of California Red-legged Frogs (Tatarian 2008), and suggests that Muir may have been describing California Red-legged Frogs 40 y before the Yosemite survey transect was conducted.

Early 20th century: The Yosemite Survey Transect.—From 1914–1920, with a team of zoologists from the University of California, Grinnell and Storer (1924) surveyed a nearly 2500-km^2 transect across the Sierra Nevada and through Yosemite National Park. They documented 7 species of amphibians (Grinnell and Storer 1921) and identified 1 locality for California Red-legged Frogs in the transect's western region (Snelling, California; 25 May 1915), but the exact location of the collection site was not specified (Grinnell and Storer 1924; Barry and Fellers 2013). Based on Storer's unpublished field notes and historical topographic maps for the period, Jennings and Hayes (1994) determined that this collecting location was at the Montgomery Street crossing of Ingalsbe Slough in Merced County (42-m elevation). Grinnell and Storer (1924) concluded that the California Red-legged Frog is "more wary than the Yellow-legged Frog and often escapes observation by reason of this fact" (Appendix Table 2). The single California Red-legged Frog recorded by Grinnell and Storer (1924) was brought to them by an acquaintance and not collected by a team member of the survey, suggesting that the survey team was not strongly focused on amphibians.

Mid-20th century.—Herpetologist Ernest Karlstrom examined amphibians and their distributions in the Sierra Nevada, and conducted natural history research with California Toads in Yosemite Valley at Ahwahnee Meadow from 1954–1955 (Karlstrom 1962). Karlstrom's work was most intensively focused in a 100-m^2 area of Ahwahnee Meadow, on the eastern end of Yosemite Valley, and did not include habitats where most ranids would have been observed (i.e., nearer the Merced River, creeks, and side channel pools). Karlstrom noted that Foothill Yellow-legged Frogs were a rare occurrence in the Merced River (Appendix Table 1), and while this suggests that Karlstrom is referring to the portion of the river nearest his study site, it is unclear to what he was actually referencing (Karlstrom 1962). Foothill Yellow-legged Frogs were observed at 3 separate Merced River localities in the Valley in the 1940s and 1970s (Appendix Table 1). Karlstrom was among the first to raise the alarm that the Bullfrogs in Yosemite Valley would be detrimental to native aquatic fauna (Karlstrom 1962).

Bullfrog invasion.—Bullfrogs were well-established in the California Central Valley by 1930 (Storer 1933), and the 1st specimen from the Sierra Nevada foothills was collected in 1923 (VertNet 2019). Bullfrogs eventually became established at 2 sites within Yosemite National Park: Yosemite Valley and the Swamp Lake area (US National Park Service 2012). A 1946 report of reptiles and amphibians in Yosemite did not include the presence of Bullfrogs (Walker 1946), suggesting the species was still absent at that time. The 1st Bullfrog in Yosemite Valley was likely introduced to the Ahwahnee Hotel reflecting pool sometime in the early 1950s (Garland 1997; D Estrada, Ahwahnee Hotel, Yosemite Valley, California, pers. comm.), and the 1st published Valley Bullfrog observation is from the Ahwahnee Hotel reflecting pool in 1955

(Richards 1958). In 1956, Karlstrom collected the 1st Bullfrog specimen from Yosemite Valley, adjacent to the Ahwahnee reflecting pool at Ahwahnee Meadow (Appendix Table 1).

In the early 1960s, the expansion of Bullfrogs into the Sierra Nevada was cause for concern among herpetologists, who warned that it would have a catastrophic impact on native anurans (Cunningham 1960; Karlstrom 1962; Basey 1972; Appendix Table 2). By the early 1970s, Bullfrogs were rapidly replacing native frog populations, especially Foothill Yellow-legged Frogs, in most foothill localities (Moyle 1973). In the mid-1970s, Foothill Yellow-legged Frogs were observed in the west end of Yosemite Valley at Fern Spring and from mid-valley at the bottom of Indian Canyon (D Graber, Yosemite National Park, pers. comm., Appendix Table 1); at that time, Bullfrogs were only known from near the Ahwahnee Hotel reflecting pool. In 1973, a 2nd Bullfrog specimen was collected in Yosemite Valley near Camp 9–950 m from the Ahwahnee reflecting pool (Appendix Table 1).

Though Bullfrogs were present in the Valley in the late 1970s, they may not yet have been abundant. Responding to an inquiry about the possibility of a Bullfrog harvest in Yosemite Valley, a park biologist stated that Bullfrogs were very few at that time (Keay 1979; Appendix Table 2). The slow initial spread of Bullfrogs may have been due to the Valley's elevation, as higher elevation populations of the species have been observed dispersing more slowly (Flynn and others 2017). Bullfrogs were also observed in other parts of Yosemite by the early 1970s (Basey 1972).

In the 1980s, Bullfrogs at the Ahwahnee Hotel reflecting pool were in notably high abundance (D Estrada, Ahwahnee Hotel, pers. comm.), and the species became well-established throughout Yosemite Valley by the 1990s (Drost and Fellers 1996). In Yosemite, Swamp Lake, Miguel Meadows, and Gravel Pit Lake all had California Red-legged Frogs at one time (Appendix Table 1). Today, Bullfrogs are the only ranids present at these sites (Barry and Fellers 2013; RLG, unpubl. data). In the fall of 1997, one Yosemite biologist began sporadic Bullfrog removals in the Valley until a more systematic effort was funded and consistently employed beginning in 2005; successful eradication was achieved in 2018 (Kamoroff and others 2020).

California Red-legged Frogs in the Greater Yosemite Region.—California Red-legged Frogs could be observed in abundance in the Sierra Nevada foothills at one time. Commercially harvested California Red-legged Frogs were reported in the San Francisco fish markets as coming from 300 km east of the city in "Four Creeks Area," in the current vicinity of Visalia (Lockington 1879). A number of California Central Valley and Sierra Nevada foothill California Red-legged Frog records used to assess the species' distribution in Jennings and Hayes (1994) were reported as frogs collected to be eaten on camping trips or sold as biological specimens for high school dissecting classes during the 1940s and 1950s. Walker (1946) reported that California Red-legged Frogs were commercially harvested outside of Yosemite.

The earliest California Red-legged Frog specimen from our study area was collected in 1922 at Camp Mather (Appendix Table 1). Four California Red-legged Frog specimens reportedly collected from the site in 1924 are missing from the Yosemite Museum collections (Appendix Table 1). In 1931, a published key to the amphibians and reptiles of the Yosemite region did not include the Camp Mather specimens (King 1931), so the locality may have remained rather obscure because of its location outside of park boundaries. The last California Red-legged Frog records from Camp Mather were 10 individuals collected in 1945 (Appendix Table 1). The species has been absent from the site since at least 1995 (US National Park Service 2000b). It is unknown when California Red-legged Frogs were extirpated from Camp Mather; however, Bullfrogs have since invaded. Twenty-two Bullfrogs were collected in 2004 (VertNet 2019), likely soon after they became established, and the species is still present at the site, where eradication efforts are currently underway. The 1st California Red-legged Frog specimen from Yosemite National Park was collected at Swamp Lake in 1938 (Appendix Table 1). A report from that survey suggests why California Red-legged Frogs may have escaped notice before then: "This frog is much more secretive in its habits than the Sierra Yellow-legged Frog. Beyond doubt, this fact is important in its previous exclusion from amphibian check lists" (Yosemite Field School 1938; Appendix Table 2).

Several California Red-legged Frogs were collected from Swamp Lake in successive years. Three individuals were collected in 1939, though these were originally misidentified as Foothill Yellow-legged Frogs (Yosemite Field School 1939); 15 were collected in 1940, including 2 large adult females (Yosemite Field School 1940); and 3 in 1941 (Yosemite Field School 1941; Appendix Table 1). Although large numbers of specimens were not collected in 1941, the species was apparently widely distributed. The Yosemite Field School (1941) reported that California Red-legged Frogs were observed at " almost every lakelet in the district," (Appendix Table 1) including Gravel Pit and Swamp Lakes, as well as numerous other small lakes in the vicinity.

No California Red-legged Frog observations from Swamp Lake were located after 1949 (Basey 1978) and when Yosemite biologists observed the species there in 1974 (D Graber, pers. comm.). Bullfrogs, but not California Red-legged Frogs, were observed at Swamp Lake in 1975 (Basey 1978), and no California Red-legged Frogs have been observed there since (D Graber, pers. comm.; RLG, unpubl. data; Appendix Table 1). Large numbers of Bullfrogs and no California Red-legged Frogs were observed at Swamp Lake during resurveys in 1997 (Barry and Fellers 2013; Appendix Table 1), and no California Red-legged Frogs were observed during extensive day and night Bullfrog removal efforts by Yosemite biologists from 2017–2022 (RLG, unpubl. data). Despite the presence of Bullfrogs, the site still supports adequate breeding habitat for California Red-legged Frogs (Barry and Fellers 2013; RLG, unpubl. data), and is a proposed reintroduction site for the species. Though Bullfrog eradication is notoriously difficult, the hydrology of Yosemite Valley facilitated their successful eradication there (Kamoroff and others 2020), and the Miguel Meadow Complex has similar constraints to recolonization.

Storer (1915) was interested in the Smith Creek area because of its unique biodiversity and "peculiar mixture of Upper Sonoran and Transition zone species", the same description attributed to the unique biological complexity of the Swamp Lake area (Grinnell and Storer 1924; Yosemite Field School 1938). During the Yosemite surveys of 1915–1916, he noted that Foothill Yellow-legged Frogs were fairly common in Smith Creek, and California Red-legged Frogs were present, although uncommon (Storer 1915). Grinnell and Storer (1924) reported a 2nd-hand observation for California Red-legged Frogs in the Yosemite transect at "Smith Creek, 6 mi [9.7 km] northeast of Coulterville." One California Red-legged Frog specimen (Appendix Table 1) was collected from Jordan Creek (about 2 km northeast of the Smith Creek location), 808-m elevation, in 1967 (Basey 1978). Bullfrogs, but not California Red-legged Frogs, were observed in the Smith Creek-Jordan Creek area during surveys in 1976–1978 (Basey 1978). As recently as 1984, 4 California Red-legged Frogs were recorded at Smith Creek (Appendix Table 1); however, a 1993 resurvey of the Grinnell transect revealed that California Red-legged Frogs had been extirpated from this locality (Drost and Fellers 1994).

At Piney Creek, California Red-legged Frogs were observed in 1972, with an approximately equal abundance of Bullfrogs (Basey 1978). California Red-legged Frogs were also observed in 1974 (Barry and Fellers 2013), and the most recent observation was in 1984, when 1 adult and 2 Bullfrogs were observed (R Hansen, Herpetological Review, pers. comm.). During a drought in 1975–1977, the stream went nearly dry, and California Red-legged Frogs were not observed at the site during surveys in 1975–1978 (Basey 1978). In 1990, only Bullfrogs were observed during day and night surveys, and 1 Bullfrog was collected as a voucher specimen (Appendix Table 1). In subsequent resurveys in 1993 and 1994, only Bullfrogs were observed at the site (Appendix Table 1). In 2017, Park Service biologists visited the portion of Piney Creek where R Hansen had observed California Red-legged Frogs in 1984. Only Bullfrogs were observed.

Four California Red-legged Frogs were collected in Woods Creek in 1950, but when the site was revisited in the late 1970s, only Bullfrogs were observed. Zweifel (1953) noted that California Red-legged Frogs were extremely abundant in Willow Creek, 70 km south of Yosemite Valley in the Sierra Nevada foothills near the San Joaquin Experimental Range (Appendix Table 1). This is the only post-1900 record that notes high abundance of this species outside of southern California or the Coast Ranges. As it was a daytime observation, it is likely that most of the frogs were juveniles, which would partially explain the high abundance. Bullfrogs were 1st

introduced to the San Joaquin Experimental Range in 1934 and rapidly expanded into the surrounding drainages (Cohen and Howard 1958). When MRJ revisited the location 35 y after Zweifel's observation, only Bullfrogs could be found, and naturalists currently at the San Joaquin Experimental Range had not heard of California Red-legged Frogs occurring there in the past.

Paucity of Reliable Records

Species occurrence records are inherently biased subsamples of ecosystems and communities (Behrensmeyer and others 2000), and smaller species are more frequently data deficient (Crees and others 2019). The dearth of information available about the historical distribution and occurrence of amphibians in Yosemite Valley is unexpected, given its popularity and the extent of survey efforts by highly skilled naturalists in the Yosemite region as noted above. Collecting and observation bias as a result of general disinterest in herpetofauna may have contributed to this trend. We found evidence for 3 primary causes of the relative lack of Yosemite Valley amphibian records: (1) Yosemite's emphasis on sportfishes and game species over nongame wildlife prior to the 1960s; (2) bird and mammal study bias that favored the collection and recording of natural history observations for these taxa over herpetofauna by naturalists, including diurnal as opposed to nocturnal surveys and other logistical challenges of collecting amphibians and reptiles; and (3) extensive habitat alteration in Yosemite Valley in the early 20th century.

Collecting challenges and observation bias.—Challenging logistics requiring pack stock for collecting expeditions likely contributed to the dearth of amphibian and reptile specimens collected during the Yosemite Survey Transect and surveys conducted by the Yosemite Field School. Specimens of fishes are also limited from backcountry areas during this time (Fishnet2 Portal, www.fishnet2.net, 5 February 2021). Backcountry travel using pack stock for collecting expeditions demanded "time, effort, and perseverance" (Storer and others 2004). The time required to use horses and pack animals is extensive, and the weight capacity for carrying supplies (for example, canvas tents, rifles, snap traps, provisions) was limited. The alcohol solution used to preserve amphibians and reptiles would increase volume and weight dramatically, and containers such as wooden barrels were bulky and heavy. Therefore, more effort was likely put into trapping small mammals and shooting or observing birds.

Considerable records for sympatric aquatic herpetofauna would be expected if Grinnell and Storer thoroughly surveyed for amphibians in Yosemite Valley from 1914–1920. Conversely, we found several indications that the expeditions did not extensively survey aquatic habitats for amphibians. Grinnell and Storer (1924) report these common aquatic and semi-aquatic herpetofauna species from Yosemite Valley: (1) 2 California Toads, despite that this species was among the more common Yosemite Valley anurans into the mid-1950s (Karlstrom 1962); (2) "Scores" of Chorus Frogs, from a single grassy swale; and (3) 1 Garter Snake (*Thamnophis* spp.), from near the Valley wall, away from water (Grinnell and Storer 1924). Perhaps due to the species' relative ubiquity, Chorus Frogs were not often recorded by Grinnell and Storer unless recognition of the species accompanied an unusual natural history observation (Drost and Fellers 1996).

The Grinnell and Storer (1924) surveys of amphibians and reptiles have been described as "haphazard at best," being only observational and lacking systematic survey methods (Moritz and others 2011; Appendix Table 2). The paucity of amphibian records in Grinnell and Storer (1921, 1924) may reflect their strong emphasis on birds and mammals, for which they conducted extensive and detailed transects within Yosemite Valley (Grinnell and Storer 1924). This propensity was repeated during the Grinnell resurveys conducted from 2003–2005, in which the amphibian and reptile surveys were conducted "mostly as targeted searches" in suitable habitat, and from driving on roads (Moritz and others 2011). The most common anuran species across all Yosemite sites in this resurvey, the Chorus Frog, was not reported from Yosemite Valley (Moritz and others 2011), indicating that aquatic habitats were likely under-sampled.

The Yosemite Field School was a summer program established in 1925 to fill a need for highly trained naturalists and nature guides in Yosemite National Park and nationally (Bryant 1927). For nearly 30 y, Yosemite Field School students conducted comprehensive surveys at 1

of the 2 research reserves established in Yosemite: Boundary Hill and Swamp Lake. The instructors of the Yosemite Field School were Yosemite staff naturalists and naturalist rangers, in conjunction with experts from universities and government agencies, including naturalists Joseph Dixon, Robert Usinger, James Cole, and Robert Stebbins (Yosemite Field School 1940; Russell 1968). Our review of the Yosemite Field School archives, research reserve reports, and Joseph Dixon correspondence suggests that the primary focus of the curriculum was toward plants, birds, mammals, and geology. On the amphibians and reptiles of the Swamp Lake area, the class of 1939 reported that they did not intensively study the amphibians there (Yosemite Field School 1939; Appendix Table 2). Yosemite Field School classes, 1938–1941, observed Chorus Frogs at Swamp Lake, but none were collected (Yosemite Field School 1941; Yosemite Museum Collections Records).

Personnel involved in conducting the surveys may have been just as important. The Yosemite Field School Class of 1938 observed California Red-legged Frogs in the park for the first time at Swamp Lake, and suggested that the cryptic nature of the species was cause for earlier lack of detection (Yosemite Field School 1938; Appendix Table 2). The following year, several California Red-legged Frogs were misidentified as Foothill Yellow-legged Frogs and Sierra Nevada Yellow-legged Frogs (Yosemite Field School 1939). Conversely, in 1940, the year that Robert Stebbins, who would subsequently become a foremost authority on western USA amphibians and reptiles (Stebbins 2003), was on the Yosemite Field School faculty, students collected 13 specimens and only 1 (a Foothill Yellow-legged Frog that was later reassigned as a California Red-legged Frog) was misidentified (Yosemite Field School 1940; Yosemite Museum Collections Records; Appendix Table 1). In 1941, the students concluded that night collecting in future years would likely produce more amphibian and reptile records (Appendix Table 2), indicating that the students rarely, if ever, conducted night surveys, and pointing to a source of observation bias in surveys that were focused on birds, mammals, and plants. Field notes from the same expedition reveal that many of the lizard specimens were incidental captures in small mammal traps (Storer 1915), and the 2 specimens (including the type) for the celebrated Yosemite plethodontid, the Mount Lyell Salamander (*Hydromantes platycephalus*), was collected accidentally in the same way (Camp 1916). Without nighttime surveys, amphibians, especially the primarily nocturnal California Red-legged Frog (Hayes and Tennant 1985; Fellers and Kleeman 2006), are much less likely to be observed. Storer (1925) also noted that surveys were not typically conducted at night, and this probably limited knowledge of the California Red-legged Frog's distribution (Appendix Table 2).

The utility of historical ecology for conservation is predicated upon natural resource managers' and institutions' awareness of their own histories and shifting approaches (Szabó 2010). Over time, the US National Park Service has had to balance developing parks for visitor enjoyment with the ecological management of natural resources (Sellars 1997; Mazur 2015). Yosemite Valley was the site of a fish hatchery from 1919–1956, which drew many visitors to its non-native fish interpretive programs (Bingaman 1961). Yosemite biologists in the 1950s and 1960s were focused on hatchery priorities and game species, primarily deer and bears (Yosemite Archives Natural Resource Management Records, collection 1011). Coincident with the publication of "Silent Spring" (Carson 1962) and increased public concern for aquatic ecosystems, Yosemite administrators struggled to de-emphasize the park's non-native fish interpretation program in favor of aquatic ecology programs focused on native species (US National Park Service 1963; Appendix Table 2).

In the early 1970s, Peter Moyle evaluated the distribution of Bullfrogs relative to native amphibians in the San Joaquin Valley and adjacent Sierra Nevada (Moyle 1973). Moyle requested information from Yosemite about Foothill Yellow-legged Frogs, California Red-legged Frogs, and Bullfrogs on the floor of the Valley. In response, Yosemite biologist William Jones said that the park had inadequate information to determine whether the Bullfrog was replacing Foothill Yellow-legged Frogs in Yosemite Valley, and that Moyle's letter reiterating Karlstrom's findings that the Bullfrogs were spreading from the Ahwahnee Hotel reflecting pool was the first he had heard of the phenomenon, noting that due to a lack of interest in the park's amphibians and reptiles, the records were likely incomplete (Jones 1971, 1972; Moyle 1973;

Appendix Table 2). By the late 1970s, however, Yosemite was beginning to recognize the ecological value of its herpetofauna. Responding to a request that the park protect the often-disdained rattlesnakes in addition to the rest of the flora and fauna, the acting superintendent acknowledged that reptiles and amphibians deserve equal protection (Wolfe 1977; Appendix Table 2).

The paucity of museum specimens of the most common Yosemite Valley amphibian species, California Toads and Chorus Frogs, indicate that the Valley floor was extremely under-sampled for amphibians between 1911 and 1955. In that time period, 56 Chorus Frog specimens were collected, mostly in meadows; 53% of these (30/56) were collected by Karlstrom while conducting his research from 1954–1955. Similarly, of the 84 California Toad specimens collected from the Valley between 1915 and 1955, 70 (83%) were collected by Karlstrom, who also obtained specimens by paying children 25 cents per toad to collect them for him (D Hartesveldt, pers. comm.). Some of these animals were later used for radiation tagging studies (Karlstrom 1957, 1958) and thus were not kept as museum voucher specimens.

By the time collecting trends were increasing (after 1965), detectability would have already begun to decrease in step with amphibian population declines, including those that were due to the arrival of Chytrid to the Sierra Nevada in the 1960s and 1970s (Green and Kagarise Sherman 2001; J Van Wagtendonk, Yosemite National Park, pers. comm.). When the National Park Service began taking sharp notice to the widespread amphibian disappearances being reported, over 60 y of missed opportunity to survey and establish baselines had passed. Nearly all of the Stanford University and California Academy of Sciences amphibian collections were lost in the 1906 San Francisco earthquake and fire that destroyed the latter institution (Burt and Myers 1942; Jennings 1997); therefore, specimens collected prior to this date have not been accounted for in this study.

The only specimen records for Sierran Newt from Yosemite Valley are 2 individuals collected in 1895, and 4 in the 1930s. Walker (1946) thought the relative scarcity of Sierran Newt collections in the Valley, as compared to the Swamp Lake, Vernon Lake, and Laurel Lake areas of Yosemite, was not a "true index of distribution but rather a result of conditions favorable for collecting," suggesting that the Valley had more adverse collecting conditions than other sites. Large numbers of visitors may have impelled biologists to search in more inaccessible regions of Yosemite. It is perhaps not surprising that naturalists interested in documenting undisturbed wildlife would intentionally avoid the visitor bustle. Wright and others (1933) described the park as unique for its significant "wild-life problems": a large resident human population combined with thousands of cars that restrict wildlife movement in and out of the Valley (Appendix Table 2).

Historical Habitat Alteration in Yosemite Valley

The removal of indigenous people and near-cessation of cultural burning practices brought the first large ecological changes to the Valley after the initial establishment of Yosemite as a park. Mounting tourism created continual demand for infrastructure construction and improvements in the ensuing decades, leading to extensive aquatic habitat alteration that is in the process of being restored today. Past river channel management, combined with mosquito abatement practices and heavy visitor use, resulted in a much-changed aquatic landscape in the Valley.

Throughout California and the Sierra Nevada, indigenous cultural burning practices have maintained a complex mosaic of vegetation in riparian areas, keeping meadows open from encroachment by conifers and woody shrubs (Aldern and Goode 2014). Cultural burning increases small mammal and herpetofaunal diversity in central California riparian systems (Hankins 2009). Various traditional practices (for example, small-scale burning, gathering, and tending native plants) have persisted to the present day in small areas where native people are still present in the Valley; however, development, visitor use, and premature meadow drying, as well as large-scale reduction in burning, have significantly diminished the influence of these practices on Valley aquatic ecosystems (W Willis, pers. comm.).

The extensive meadow and wetland areas that once covered much of the floor of the glacially-carved Valley also provided mosquito breeding habitat (Gibbens and Heady 1964). In 1879, Galen Clark, the 1st custodian of the park,

blasted a deeper channel for the Merced River through the El Capitan moraine, lowering the water table several feet into the Valley floor (Milestone 1979). Meadows were tiled to encourage drainage for livestock grazing and human habitation. Elevated roadways diverted water away from wetlands, flooding non-suitable habitat in other areas by inhibiting surface flow (Gibbens and Heady 1964). Channel excavation (dredging of sand, debris, silt, rock, and gravel) began in the 1880s, and 3 major bridges were constructed in the early 1930s, further requiring erosion control and mitigation (Greene 1987). Extensive stream work conducted between 1928 and 1938 included sloping and revegetating undercut riverbanks, and erosion control measures such as revetments, channel clearing, and clearing of debris and log jams from channels (Gibbens and Heady 1964; Greene 1987). Today, large trees that fall into the designated Merced River rafting area and upstream of bridges are still bucked and moved to the river banks to clear the way for this recreational activity and protect infrastructure (US National Park Service 2014). Simultaneously, many sections of the Merced River are continually being restored, creating more favorable habitat for amphibians and other wildlife.

In addition to infrastructure impacts, visitor use historically impacted aquatic habitats in the Valley. The popularity of the banks of the Merced River for picnic and swimming areas caused severe trampling, soil compaction, and vegetation removal, increasing surface runoff and erosion (Gibbens and Heady 1964). Riparian vegetation in the Valley was trampled so badly by visitors between 1916 and 1919 that it widened the Merced River channel by 27–100% in some areas (US National Park Service 2014). Since Wild and Scenic River designation of the Merced in 1987, Yosemite has reduced impacts by redirecting visitor use and establishing riparian buffers for development, in addition to other restoration activities (US National Park Service 2014).

To control mosquitoes in Yosemite Valley, oil was applied to wetlands and other standing water (Karlstrom 1962; Greene 1987). Wright and others (1933) observed dead, oiled birds in pools and meadows, and floating down the Merced River (Appendix Table 2). Amphibians' permeable skin makes them highly susceptible to adverse effects from toxicants (Egea-Serrano and others 2012). In 1954, the oil application practice resulted in mortality of larval Chorus Frogs and California Toads at Stoneman Meadow in Yosemite Valley (Karlstrom 1962).

Natural forces have also altered aquatic habitat in Yosemite Valley. Beavers (*Castor canadensis*) are present in the Valley today, and may have occupied the Valley prior to their widespread reintroduction to the Sierra Nevada in the 1940s. Historical records for Beavers in the Valley are lacking, perhaps because, like California Red-legged Frogs, their overharvest (by the 1840s) greatly predates the establishment of any comprehensive specimen collections in California (Jennings and Hayes 1985; Lanman and others 2012). Beaver dams slow the flow of water and create habitat for amphibians that require slow-moving water and pools for breeding (Romansic and others 2021). If Beavers did occupy Yosemite Valley in the past, they would have created habitats with adequate vegetative and bottom cover with protection from scouring flows that California Red-legged Frogs require for breeding in foothill streams. Beavers are currently creating this habitat type in Yosemite Valley at 2 release sites where California Red-legged Frogs have persisted since their initial 2016 translocation.

These extensive stream alterations have all served to effectively shift ranid habitat suitability in the Valley. Amphibians, particularly Foothill Yellow-legged Frogs and California Red-legged Frogs, are sensitive to flow alterations and habitat degradation (US Fish and Wildlife Service 2002; Kupferberg and others 2012). California Red-legged Frogs require overhanging banks for cover and emergent vegetation on which to attach egg masses, and prefer shady, vegetated habitats with deeper pools. Conversely, Foothill Yellow-legged Frogs breed exclusively in flowing water and prefer shallow, riffle-pool cobble substrates with open areas for basking (Tatarian 2008; Kupferberg and others 2012). Historical habitat alteration rendered the Yosemite Valley floor more suitable for California Red-legged Frogs than Foothill Yellow-legged Frogs. Nevertheless, Yosemite Valley tributaries, as well as areas upstream and downstream of Yosemite Valley, likely provide suitable habitat for Foothill Yellow-legged Frogs, while the Merced River can still provide a geneflow corridor.

Conclusion

Historical baselines have customarily been used with the assumption that little to no environmental change has occurred from the baseline to the present. Here, we have shown that Yosemite Valley has changed significantly since its establishment as a national park. We also found limited evidence for California Red-legged Frog occurrence in Yosemite Valley, and that inattention to amphibians, in concert with acute ecosystem alteration and the introduction of non-native Bullfrogs, are implicated in the scarcity of comprehensive historical information for California Red-legged Frog occupancy.

A reference frame more appropriate than historical baselines in a changing world is to evaluate what would have happened without the intervention of reintroduction and associated restoration efforts (i.e., counterfactuals; Bull and others 2014). Without the goal of introducing California Red-legged Frogs to provide a safe harbor for them in the face of ongoing threats, the impetus for the massively challenging undertaking of eradicating Bullfrogs is unlikely to have occurred, and this highly invasive species would be continuing to cause detriment to native fauna (Cunningham 1960). Chorus Frogs have returned in numbers not observed since before the Bullfrog invasion (RLG, unpubl. data). The initial introduction of California Red-legged Frogs to the Valley in 2016 led to subsequent successful breeding and recruitment in 2019–2022. In 2022, the 1st adult progeny of zoo-reared California Red-legged Frogs successfully colonized and bred in an area where they were not introduced, and that breeding site exhibits very high survival and recruitment. Translocating this species to the upper end of its known elevational occurrence may assist in adaptation to a changing climate (Butt and others 2021). Yosemite Valley now provides a safe harbor on protected public lands for future reintroductions of the species elsewhere in the region.

The conservation translocation of California Red-legged Frogs to Yosemite Valley has allowed for integration of the complexities of change over time rather than focusing on restoration to an imagined, ideal environment in the past (Alagona and others 2012; Forbes and others 2020). Conservation introductions have a role in highly impacted ecosystems, where landscapes may have changed to be no longer suitable for 1 native species, but are more suitable for another, despite being outside of its historical range (Moyle 2014).

Perhaps not coincidentally, the moment that amphibian species were starting to decline was precisely when a broader interest in their natural history began to grow (Stebbins 1966). Many amphibians were in catastrophic decline before an organized effort to examine the causes were underway (Mendelson 2011; Adams and others 2017a), demonstrating the need for historical ecology to fill these gaps in understanding through time. Amphibians have been a casualty of "too little, too late" conservation in the past. Today, applying conservation translocations to restoration targets informed, but not limited by, historical ecosystems can orient threatened species toward a trajectory for recovery in an uncertain future.

Acknowledgments

Various tribal members, including 7 tribes and groups traditionally associated with Yosemite, live and work in the Valley and neighboring communities. Their voices are an important part in the continued management of natural and cultural resources, including research on various species of wildlife, as well as traditional practices that contribute to the ecological landscape. We thank G Cox, D Estrada, D Graber, R Hansen, D Hartesveldt, R Knapp, S Kupferberg, A McKinney, G Pauly, R Peek, P Rogers, V Sanchez, J Van Wagtendonk, and W Willis for their assistance, and P Alagona, C Davidson, R Hansen, and R Mazur for their comments on previous versions of the manuscript. Permission to copy and publish information from the field notes of T Storer were granted to MRJ by R Storer. This research was funded by the Dorrance Family Foundation and the Yosemite Conservancy.

Literature Cited

*Adams AJ. 2022. Surveys for amphibian Chytrid fungus (*Batrachochytrium dendrobatidis*) in the Santa Monica Mountains National Recreation Area at California Red-legged Frog (*Rana draytonii*) source and translocation sites, 2020–2021. Thousand Oaks, California: Prepared for US National Park Service. 10 p.

Adams AJ, Bushell J, Grasso RL. 2022. To treat or not to treat? Experimental pathogen exposure, treatment, and release of a threatened amphibian. Ecosphere 13:e4294.

* Unpublished

Adams AJ, Pessier AP, Briggs CJ. 2017a. Rapid extirpation of a North American frog coincides with an increase in fungal pathogen prevalence: Historical analysis and implications for reintroduction. Ecology and Evolution 7:10216–10232.

Adams AJ, Kupferberg SJ, Wilber MQ, Pessier AP, Grefsrud M, Bobzien S, Vredenburg VT, Briggs CJ. 2017b. Extreme drought, host density, sex, and Bullfrogs influence fungal pathogen infection in a declining lotic amphibian. Ecosphere 8:e01740.

Adams AJ, Pessier AP, Cranston P, Grasso RL. 2020. Chytridiomycosis-induced mortality in a threatened anuran. PLoS One 15:e0241119.

Alagona PS, Sandlos J, Wiersma YF. 2012. Past imperfect. Environmental Philosophy 9:49–70.

Aldern JD, Goode RW. 2014. The stories hold water: Learning and burning in North Fork Mono homelands. Decolonization: Indigeneity, Education and Society 3:26–51.

Amphibiaweb. 2020. *S*: Common frog. [Online]. Berkeley, CA: University of California. http://amphibiaweb.org/species/5168. Accessed 25 February 2020.

Badè WF, Muir J. 1924. The life and letters of John Muir (Volume 9). Houghton Mifflin. 452 p.

Barrett SA. 1919. Myths of the Southern Sierra Miwok. University of California Publications in American Archaeology and Ethnology 16:1–28.

Barry SJ, Fellers GM. 2013. History and status of the California Red-legged Frog (*Rana draytonii*) in the Sierra Nevada, California, USA. Herpetological Conservation and Biology 8:456–502.

Basey HE. 1972. Bullfrogs and the environment. Bulletin of the Yosemite Natural History Association 42:4.

*Basey HE. 1978. The status of the Red-legged Frog in interior California: Report to the California Department of Fish and Game. Modesto, CA: Modesto Junior College. 10 p.

Basey HE. 1991. Discovering Sierra reptiles and amphibians. Yosemite National Park, CA: Yosemite Association. 56 p.

Becker CG, Fonseca CR, Haddad CFB, Batista RF, Prado PI. 2007. Habitat split and the global decline of amphibians. Science 318:1775–1777.

Behrensmeyer AK, Kidwell SM, Gastaldo RA. 2000. Taphonomy and paleobiology. Paleobiology 26:103–147.

Bennyhoff JA. 1956. An appraisal of the archaeological resources of Yosemite National Park. Berkeley, CA: University of California Archaeological Survey. 106 p.

Bingaman JW. 1961. Guardians of the Yosemite: A story of the first rangers. Palm Desert, CA: Desert Printers. 152 p.

Bradford DF. 1991. Mass mortality and extinction in a high-elevation population of *Rana muscosa*. Journal of Herpetology 25:174–177.

Brown C, Nowakowski AJ, Keung NC, Lawler SP, Todd BD. 2021. Untangling multi-scale habitat relationships of an endangered frog in streams to inform reintroduction programs. Ecosphere 12:e03799.

Brown C, Wilkinson LR, Wilkinson KK, Tunstall T, Foote R, Todd BD, Vredenburg VT. 2019. Demography, habitat, and movements of the Sierra Nevada Yellow-Legged Frog (*Rana sierrae*) in streams. Copeia 107:661–675.

Bryant HC. 1927. The Yosemite School of Field Natural History: A National Park Service educational activity. Yosemite Nature Notes 6:1–8.

Bull JW, Gordon A, Law EA, Suttle KB, Milner-Gulland EJ. 2014. Importance of baseline specification in evaluating conservation interventions and achieving no net loss of biodiversity. Conservation Biology 28:799–809.

Burt CE, Myers GS. 1942. Neotropical lizards in the collection of the Natural History Museum of Stanford University. Stanford University Publications: Biological Sciences 8:273–324.

Butt N, Chauvenet ALM, Adams VM, Beger M, Gallagher RV, Shanahan DF, Ward M, Watson JEM, Possingham HP. 2021. Importance of species translocations under rapid climate change. Conservation Biology 35:775–783.

Camp CL. 1916. *Spelerpes platycephalus*, a new alpine salamander from the Yosemite National Park, California. University of California Publications in Zoology 17:11–14.

Carson R. 1962. Silent spring. New York, NY: Houghton Mifflin. 378 p.

Cohen NW, Howard WE. 1958. Bullfrog food and growth at the San Joaquin Experimental Range, California. Copeia 1958:223–225.

Collins JP. 2010. Amphibian decline and extinction: What we know and what we need to learn. Diseases of Aquatic Organisms 92:93–99.

Coombes SC. 1902. Frog-raising; As good and better than many gold mines; the only book in the whole wide world on the cultivation, development, and various uses of the common Edible Frog; how to breed and feed it, and how to protect it from its enemies, etc. San Francisco, CA: Self-published. 24 p.

Crees JJ, Collen B, Turvey ST. 2019. Bias, incompleteness and the 'known unknowns' in the Holocene faunal record. Philosophical Transactions of the Royal Society B 374:20190216.

Cunningham JD. 1960. Additions to the vertebrate fauna of Yosemite. Yosemite Nature Notes 39:37.

Cushman SA. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128:231–240.

Davidson C. 2004. Declining downwind: Amphibian population declines in California and historical pesticide use. Ecological Applications 14:1892–1902.

Davidson C, Shaffer HB, Jennings M. 2001. Declines of the California Red-legged Frog: climate, UV-B, habitat, and pesticides hypotheses. Ecological Applications 11:464–479.

Dowie M. 2009. Conservation refugees: The hundred-year conflict between global conservation and native peoples. Cambridge, MA: The MIT Press. 373 p.

*Drost CA, Fellers GM. 1994. Decline of frog species in the Yosemite section of the Sierra Nevada. Davis, CA: University of California, Davis Cooperative National Park Studies Unit. 54 p.

Drost CA, Fellers GM. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conservation Biology 10:414–425.

Egea-Serrano A, Relyea RA, Tejedo M, Torralva M. 2012. Understanding of the impact of chemicals on amphibians: A meta-analytic review. Ecology and Evolution 2:1382–1397.

Fellers GM, Kleeman PM. 2006. Diurnal versus nocturnal surveys for California Red-Legged Frogs. Journal of Wildlife Management 70:1805–1808.

Fisher RN, Shaffer HB. 1996. The decline of amphibians in California's Great Central Valley. Conservation Biology 10:1387–1397.

Flynn LM, Kreofsky TM, Sepulveda AJ. 2017. Introduced American Bullfrog distribution and diets in Grand Teton National Park. Northwest Science 91:244–256.

Forbes ES, Alagona PS, Adams AJ, Anderson SE, Brown KC, Colby J, Cooper SD, Denny SM, Hiroyasu EHT, Heilmayr R, Kendall BE, Martin JA, Hardesty-Moore M, Mychajliw AM, Tyrrell BP, Welch ZS. 2020. Analogies for a no-analog world: Tackling uncertainties in reintroduction planning. Trends in Ecology and Evolution 35:551–554.

Frey JK. 2006. Inferring species distributions in the absence of occurrence records: An example considering Wolverine (*Gulo gulo*) and Canada Lynx (*Lynx canadensis*) in New Mexico. Biological Conservation 130:16–24.

Garland FP. 1997. Yosemite takes no prisoners in war on Bullfrogs. Recordnet [Online]. https://www.recordnet.com/article/19971023/A_NEWS/310239995. Accessed 25 February 2020.

Garwood JM, Knapp RA, Pope KL, Grasso RL, Magnuson ML, Maurer JR. 2013. Use of historically fishless high-mountain lakes and streams by nearctic River Otters (*Lontra canadensis*) in California. Northwestern Naturalist 94:51–66.

Gassaway L. 2009. Native American fire patterns in Yosemite Valley: Archaeology, dendrochronology, subsistence, and culture change in the Sierra Nevada. Society for California Archaeology Proceedings 22:1–19.

Germano J, Ewen JG, Mushinsky H, McCoy E, Ortiz-Catedral L. 2014. Moving towards greater success in translocations: Recent advances from the herpetofauna. Animal Conservation 17:1–3.

Gibbens RP, Heady HF. 1964. The influence of modern man on the vegetation of Yosemite Valley. University of California, Division of Agricultural Sciences. 44 p.

Green DE, Kagarise Sherman C. 2001. Diagnostic histological findings in Yosemite Toads (*Bufo canorus*) from a die-off in the 1970s. Journal of Herpetology 35:92–103.

Greene L. 1987. Yosemite, the park and its resources: A history of the discovery, management, and physical development of Yosemite National Park, California: Historical narrative. Denver, CO: US Department of the Interior, National Park Service, Denver Science Center. 977 p.

Grinnell J, Storer TI. 1921. Reptiles and amphibians of Yosemite National Park. Handbook of Yosemite National Park. New York, NY: GP Putnam's Sons. p 175–182.

Grinnell J, Storer TI. 1924. Animal life in the Yosemite: An account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. Berkeley, CA: University of California Press. 752 p.

Hall AF. 1921. Handbook of Yosemite National Park: A compendium of articles on the Yosemite Region by the leading scientific authorities. New York, NY: Putnam. 268 p.

Halliday T. 2015. The book of frogs: A life-size guide to six hundred species from around the world. Chicago, IL: University of Chicago Press. 656 p.

Hankins DL. 2009. The effects of indigenous prescribed fire on herpetofauna and small mammals in two Central Valley California riparian ecosystems. The California Geographer 49:31–49.

Harding G, Griffiths RA, Pavajeau L. 2016. Developments in amphibian captive breeding and reintroduction programs. Conservation Biology 30:340–349.

Hayes MP, Tennant MR. 1985. Diet and feeding behavior of the California Red-Legged Frog, *Rana aurora draytonii* (Ranidae). The Southwestern Naturalist 30:601–605.

Hayes MP, Jennings MR. 1986. Decline of ranid frog species in western North America: Are Bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology 20:490–509.

*Hayes MP, Wheeler CA, Lind AJ, Green GA, Macfarlane DC. 2016. Foothill Yellow-legged Frog conservation assessment in California. General Technical Report PSW-GTR-248. Albany, CA: US Department of Agriculture, Forest Service. 193 p.

Heard M. 1904. A California frog ranch. Out West 21:20–27.

Hedges SB. 1986. An electrophoretic analysis of Holarctic hylid frog evolution. Systematic Zoology 35:1–21.

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vilà M, Zamora R, Zobel M. 2006. Novel ecosystems: Theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.

Inglis J. 1993. Traditional ecological knowledge: Concepts and cases. Ottawa, ON: International Development Research Centre. 142 p.

*IUCN. 2013. Guidelines for reintroductions and other conservation translocations. Gland, Switzerland and Cambridge, UK: IUCN/SSC Reintroduction Specialist Group. 72 p.

Jennings MR. 1988. Origin of the population of *Rana aurora draytonii* on Santa Cruz Island, California. Herpetological Review 19:76.

Jennings MR. 1995. Native ranid frogs in California. In: Laroe ET, Farris GS, Puckett CE, Doran PD, Mac MJ, editors. Our living resources: A report to the nation on the distribution, abundance, and health of US plants, animals, and ecosystems. Washington DC: USDI National Biological Service. p 131–134.

Jennings MR. 1996. Status of amphibians. Sierra Nevada ecosystem project: Final Report to Congress. Davis, CA. p 921–944.

Jennings MR. 1997. John Van Denburgh (1872–1924), pioneer herpetologist of the American West. In: Pietsch TW, Anderson WD, editors. Collection building in ichthyology and herpetology. American Society of Ichthyologists and Herpetologists. p 323–350.

Jennings MR, Hayes MP. 1985. Pre-1900 overharvest of California Red-legged Frogs (*Rana aurora draytonii*): The inducement of Bullfrog (*Rana catesbeiana*) introduction. Herpetologica 41:94–103.

*Jennings MR, Hayes MP. 1994. Amphibian and reptile species of special concern in California. Rancho Cordova, CA: California Department of Fish and Game. 255 p.

Jones WR. 1971. Letter to Peter B Moyle, November 5, 1971. El Portal, CA: Yosemite National Park Archives.

Jones WR. 1972. Letter to Peter B Moyle, March 20, 1972. El Portal, CA: Yosemite National Park Archives.

Kamoroff C, Daniele N, Grasso RL, Rising R, Espinoza T, Goldberg CS. 2020. Effective removal of the American Bullfrog (*Lithobates catesbeianus*) on a landscape level: Long term monitoring and removal efforts in Yosemite Valley, Yosemite National Park. Biological Invasions 22:617–626.

Karlstrom EL. 1957. The use of cobalt-60 as a tag for recovering amphibians in the field. Ecology 28:187–195.

Karlstrom EL. 1958. Prospecting for toads. Yosemite Nature Notes 37:134–136.

Karlstrom EL. 1962. The toad genus *Bufo* in the Sierra Nevada of California: Ecological and systematic relationships. Berkeley, CA: University of California Press. 104 p.

Keay JA. 1979. Letter from Jeffrey Keay, Wildlife Bioloigst, to JA Larrivee, June 15, 1979. El Portal, CA: Yosemite National Park Archives.

Keung NC, Lawler SP, Yarnell SM, Todd BD, Brown C. 2021. Movement ecology study of stream-dwelling Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) to inform reintroductions. Herpetological Conservation and Biology 16:72–85.

Kiesecker J, Semlitsch R. 2003. Invasive species as a global problem: Toward understanding the worldwide decline of amphibians. In: Semlitsch R, editor. Amphibian conservation. Washington, DC: Smithsonian Institution. p 113–126.

King FW. 1931. Key to the amphibians and reptiles of Yosemite National Park, California. Yosemite Nature Notes 10:91–94.

Kuchta SR. 2007. Contact zones and species limits: Hybridization between lineages of the California Newt, *Taricha torosa*, in the southern Sierra Nevada. Herpetologica 63:332–350.

Kupferberg SJ. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: The role of larval competition. Ecology 78:1736–1751.

Kupferberg SJ, Palen WJ, Lind AJ, Bobzien S, Catenazzi A, Drennan JOE, Power ME. 2012. Effects of flow regimes altered by dams on survival, population declines, and range-wide losses of California river-breeding frogs. Conservation Biology 26:513–524.

Lanman RB, Perryman H, Dolman B, James CD. 2012. The historical range of Beaver in the Sierra Nevada: A review of the evidence. California Fish and Game 98:65–80.

Lawler SP, Dritz D, Strange T, Holyoak M. 1999. Effects of introduced Mosquitofish and Bullfrogs on the threatened California Red-legged Frog. Conservation Biology 13:613–622.

Lockington WN. 1879. Notes on some reptiles and Batrachia of the Pacific Coast. American Naturalist 13:780–783.

Longcore JE, Pessier AP, Nichols DK. 1999. *Batrachochytrium dendrobatidis gen. et sp. nov.,* a Chytrid pathogenic to amphibians. Mycologia 91:219–227.

Mazur R. 2015. Speaking of bears: The bear crisis and a tale of rewildling from Yosemite, Sequoia, and other national parks. Helena, MT: Falcon Guides. 299 p.

McKelvey KS, Aubry KB, Schwartz MK. 2008. Using anecdotal occurrence data for rare or elusive species: The illusion of reality and a call for evidentiary standards. BioScience 58:549–555.

Mendelson JR III. 2011. Lessons of the lost. American Scientist 99:438–441.

Milestone JF. 1979. Yosemite Valley's forgotten natural process: The stream system. Yosemite Nature Notes 47:1–5.

Moratto M, Roper C, Hull K, Snyder J. 1999. Cultural chronology 2: The Yosemite data. Yosemite Research Center Publications in Anthropology 21:17–28.

*Moritz C, Patton JL, Conroy CJ, Leache A, Rush A, Beissinger SR. 2011. A resurvey of the Grinnell-Storer vertebrate transect through Yosemite National Park, California. Natural Resource Technical Report NPS/SIEN/NRTR—2011/439. Fort Collins, CO: US National Park Service. 152 p.

Moyle PB. 1973. Effects of introduced Bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. Copeia 1973:18–22.

Moyle PB. 2014. Novel aquatic ecosystems: The new reality for streams in California and other Mediterranean climate regions. River Research and Applications 30:1335–1344.

Muir J. 1869. Letter from John Muir to Mrs. Ezra S Carr, December 6th, 1869. In: Bade WF, editor. The life and letters of John Muir. Boston, MA and New York, NY: Houghton Mifflin. p 208.

Muir J. 1874. Letter from John Muir to Mrs. Ezra S Carr, September 27, 1874. San Marino, CA: Huntington Library.

Pearl CA, Adams MJ, Bury RB, McCreary B. 2004. Asymmetrical effects of introduced Bullfrogs (*Rana catesbeiana*) on native ranid frogs in Oregon. Copeia 2004:11–20.

Peralta-Garcia A, Hollingsworth BD, Richmond JQ, Valdez-Villavicencio JH, Ruiz-Campos G, Fisher RN, Cruz-Hernandez P, Galina-Tessaro P. 2016. Status of the California Red-legged Frog (*Rana draytonii*) in the state of Baja California, Mexico. Herpetological Conservation and Biology 11:168–180.

Recuero E, Martinez-Solano I, Parra-Olea G, Garcia-Paris M. 2006a. Phylogeography of *Pseudacris regilla* (Anura: Hylidae) in western North America, with a proposal for a new taxonomic rearrangement. Molecular Phylogenetics and Evolution 41:511.

Recuero E, Martinez-Solano I, Parra-Olea G, Garcia-Paris M. 2006b. Phylogeography of *Pseudacris regilla* (Anura: Hylidae) in western North America, with a proposal for a new taxonomic rearrangement. Molecular Phylogenetics and Evolution 39:293–304.

Richards L. 1958. Some locality records of Yosemite herps. Yosemite Nature Notes 37:118–126.

Riemer WJ. 1956. Variation and systematic relationships within the salamander genus *Taricha*. Berkeley, CA: University of California. 90 p.

Rodrigues AS, Monsarrat S, Charpentier A, Brooks TM, Hoffmann M, Reeves R, Palomares ML, Turvey ST. 2019. Unshifting the baseline: A framework for documenting historical population changes and assessing long-term anthropogenic impacts. Philosophical Transactions of the Royal Society B 374:20190220.

Romansic JM, Nelson NL, Moffett KB, Piovia-Scott J. 2021. Beaver dams are associated with enhanced amphibian diversity via lengthened hydroperiods and increased representation of slow-developing species. Freshwater Biology 66:481–494.

Russell CP. 1924. California Red-legged Frog. Yosemite Nature Notes 3.

Russell CP. 1968. 100 years in Yosemite: The story of a great national park. Yosemite National Park, CA: Yosemite Natural History Association. 210 p.

Russell RE, Halstead BJ, Mosher BA, Muths E, Adams MJ, Grant EHC, Fisher RN, Kleeman PM, Backlin AR, Pearl CA, Honeycutt RK, Hossack BR. 2019. Effect of amphibian Chytrid fungus (*Batrachochytrium dendrobatidis*) on apparent survival of frogs and toads in the western USA. Biological Conservation 236:296–304.

Sadinski W, Gallant AL, Cleaver JE. 2020. Climate's cascading effects on disease, predation, and hatching success in *Anaxyrus canorus*, the threatened Yosemite Toad. Global Ecology and Conservation 23:e01173.

Sanford P. 2019. Why we must teach the ugly side of public lands and a tool to help. [Online]. https://www.wilderness.org/articles/blog/why-we-must-teach-ugly-side-public-lands-history-tool-help. Accessed 5 January 2021.

Santana-Cordero AM, Szabó P. 2019. Exploring qualitative methods of historical ecology and their links with qualitative research. International Journal of Qualitative Methods 18:1609406919872112.

Seddon PJ. 2010. From reintroduction to assisted colonization: Moving along the conservation translocation spectrum. Restoration Ecology 18:796–802.

Sellars RW. 1997. Preserving nature in the national parks: A history. New Haven, CT: Yale University Press. 404 p.

Shaffer HB, Fellers GM, Voss SR, Oliver JC, Pauly GB. 2004. Species boundaries, phylogeography and conservation genetics of the Red-legged Frog (*Rana aurora/draytonii*) complex. Molecular Ecology 13:2667–2677.

Stebbins RC. 1966. A field guide to western reptiles and amphibians. New York, NY: Houghton Mifflin. 279 p.

Stebbins RC. 2003. A field guide to western reptiles and amphibians. New York, NY: Houghton Mifflin. 533 p.

Storer TI. 1915. Field notes: Yosemite National Park and vicinity (Yosemite 1915 expedition). Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Storer TI. 1925. A synopsis of the amphibia of California. University of California Publications in Zoology 27:1–342.

Storer TI. 1933. Frogs and their commercial uses. California Fish and Game 19:203–213.

Storer TI, Usinger RL, Lukas D. 2004. Sierra Nevada natural history: Revised. Berkeley and Los Angeles, CA: University of California Press. 412 p.

Swetnam TW, Allen CD, Betancourt JL. 1999. Applied historical ecology: Using the past to manage for the future. Ecological Applications 9:1189–1206.

Szabó P. 2010. Why history matters in ecology: An interdisciplinary perspective. Environmental Conservation 37:380–387.

Tatarian P. 2008. Movement patterns of California Red-legged Frogs (*Rana draytonii*) in an inland California environment. Herpetological Conservation and Biology 3:155–169.

US Congress. 1890. HR 12187. An Act to set apart certain tracts of land in the State of California as forest reservations. US Statutes at Large 26:650–652.

US Fish and Wildlife Service. 1996. Endangered and threatened wildlife and plants; determination of threatened status for the California Red-legged Frog. Federal Register 50 CFR Part 17:25813–25833.

US Fish and Wildlife Service. 2002. Recovery plan for the California Red-legged Frog (*Rana aurora draytonii*). Portland, OR: US Fish and Wildlife Service. 173 p.

US Fish and Wildlife Service. 2022. California Red-legged Frog (*Rana draytonii*) 5-year review: Summary and evaluation. Sacramento, CA: Sacramento Fish and Wildlife Office. 44 p.

*US National Park Service. 1963. Memorandum from Yosemite Superintendent John C. Preston to Chief of the Division of Natural History, March 14, 1963. El Portal, CA: Yosemite National Park Archives. 2 p.

*US National Park Service. 2000a. Final Yosemite Valley Plan/Supplemental Environmental Impact Statement. Yosemite National Park, CA: National Park Service. 557 p.

*US National Park Service. 2000b. Merced Wild and Scenic River: Comprehensive Management Plan and Final Environmental Impact Statement, Part 3. El Portal, CA: 549 p.

*US. National Park Service. 2012. NEPA and NHPA Clearance: 2012 Yosemite and Poopenaut Valley Bullfrog Eradication. Yosemite, CA: US Department of the Interior, Yosemite National Park. 26 p.

*US National Park Service. 2014. Merced Wild and Scenic River Final Comprehensive Management Plan and Environmental Impact Statement. El Portal, CA: Yosemite National Park. 592 p.

VertNet. 2019. Online biodiversity database [Online]. National Science Foundation. http://portal.vertnet.org/search. Accessed February 2020.

Walker M. 1946. Reptiles and amphibians of Yosemite National Park. Yosemite Nature Notes 25:1–48.

Wolf CM, Garland T, Griffith B. 1998. Predictors of avian and mammalian translocation success: Reanalysis with phylogenetically independent contrasts. Biological Conservation 86:243–255.

Wolfe JF. 1977. Letter from James F Wolfe to Bill Black, January 21, 1977. El Portal, CA: Yosemite National Park Archives.

Wright GM, Dixon JS, Thompson BH. 1933. Fauna of the National Parks of the United States: A preliminary survey of faunal relations in National Parks. Washington, DC: US Government Printing Office. 157 p.

*Yosemite Field School. 1938. Swamp Lake Research Reserve report. El Portal, CA: Yosemite National Park Archives. 49 p.

*Yosemite Field School. 1939. Yosemite Research Reserve report by Yosemite School of Field Natural History Class of 1939. El Portal, CA: Yosemite National Park Archives. 45 p.

*Yosemite Field School. 1940. Yosemite Research Reserve report by Yosemite School of Field Natural History Class of 1940. El Portal, CA: Yosemite National Park Archives. 13 p.

*Yosemite Field School. 1941. Swamp Lake Research Reserve report by the Yosemite School of Field Natural History Class of 1941. El Portal, CA: Yosemite National Park Archives. 135 p.

Yuan Z-Y, Zhou W-W, Chen X, Poyarkov NA, Jr., Chen H-M, Jang-Liaw N-H, Chou W-H, Matzke NJ, Iizuka K, Min M-S, Kuzmin SL, Zhang Y-P, Cannatella DC, Hillis DM, Che J. 2016. Spatiotemporal diversification of the true frogs (Genus *Rana*): A historical framework for a widely studied group of model organisms. Systematic Biology 65:824–842.

*Zweifel RG. 1953. Field notes: Willow Creek, O'Neals, Madera County, California. April 18, 1953. Provided by Zweifel to Mark Jennings, Davis, CA. 2 p.

Submitted 15 February 2021, accepted 26 November 2022. Corresponding Editor: Michael Parker.

APPENDIX TABLE 1. Historical ranid occurrences from the study area, with reliability scores. An explanation of the evidentiary standards is detailed in Methods. Records with an asterisk (*) after the year are new to the herpetological literature. Museum codes: AMNH = American Museum of Natural History; CUMV = Cornell University Museum of Vertebrates; MVZ = Museum of Vertebrate Zoology; OMNH = Sam Noble Oklahoma Museum of Natural History; USNM = United States National Museum; YM = Yosemite Museum.

Year	Species	Location in study area	Catalog ID/ record	N individuals	Field notes or in-text record	Source	Evidentiary standard
1869*	*Rana* spp.	Yosemite Valley	NA	unspecified	"Dainty little tree frogs occasionally climbed the ferns and made fine music in the night, and common frogs came in with the stream and helped to sing with the Hylas and the warbling, tinkling water."	Muir 1869	4
1874*	*Rana* spp.	Yosemite Valley	NA	1	"After plashing [*sic*] & lasing in the spangling crystal I swam across to examine a section of the bank & found charred bark ten feet below lake & flood deposits. In a vertical portion of the bank I discovered two small frogs of a new species each snugly nestled in a dainty [illegible] from which they could look out over the water they are not water frogs however. . .I have them in my room hoping they may sing like crickets or tree frogs for me in the night."	Muir 1874	4
1915	*Rana boylii*	Smith Creek	MVZ 5687 – 5692	6	"Boyle frogs were fairly common along a small branch of Smith Creek."	Storer 1915 VertNet 2020	1
1915	*Rana draytonii*	Smith Creek	NA	unknown	"not common"	Storer 1915; Grinnell and Storer 1924	1
1922	*Rana draytonii*	Camp Mather	USNM 312015	1		VertNet 2020;	1
1924	*Rana boylii*	Smith Creek	NA	unspecified	"Donald D. McLean reported that at Smith Creek, west of Yosemite Valley, raccoons live partly on frogs (species unnamed, but probably *Rana boylei*) (Grinnell and Storer, 1924:82)."	Karlstrom 1962	5
1924	*Rana draytonii*	Camp Mather	missing	4	"The Park Naturalist was recently surprised to find Red-legged Frogs quite abundant at Mather Station. . . Other frogs of the same species were caught and examined at the large mill pond on the same property." "The four individuals now in the Yosemite Museum were taken from a drying pond at the San Francisco Saw Mill (Mather)."	Russell 1924; Yosemite Museum Collections Records	6
1938*	*Rana draytonii*	Swamp Lake	YM 22379	1	"The first record of the California Red-legged Frog in the Yosemite National Park was obtained at Swamp Lake."	YM Collections Records, Yosemite Field School 1938	1

APPENDIX TABLE 1. Continued.

Year	Species	Location in study area	Catalog ID/ record	N individuals	Field notes or in-text record	Source	Evidentiary standard
1938	*Rana draytonii*	Swamp Lake	YM 22369	1		YM Collections Records	1
1939	*Rana sierrae*	Yosemite Valley	Observation ID: 2998	1		Yosemite Wildlife Observations Database	6
1939	*Rana draytonii*	Swamp Lake	YM 22371, 22372, 22382	3		YM Collections Records	1
1939	*Rana boylii*	Yosemite Valley	CNDDB 1979	1	"Found in pool" at Fern Spring, Yosemite Valley	California Natural Diversity Database	6
1940	*Rana draytonii*	Swamp Lake	CUMV A-0004075	1	Photograph appears in Wright & Wright 1949, plate LXXXVIII	VertNet 2020, MRJ unpublished	1
1940*	*Rana draytonii*	Swamp Lake	YM 22202, 22363, 22366-8, 22373-8, 22380, 22383	13	"These frogs were found to be fairly common where conditions were suitable for their growth and development."	YM Collections Records, Yosemite Field School 1940	1
1940	*Rana draytonii*	Swamp Lake	YM 22364	1		YM Collections Records	1
1941*	*Rana draytonii*	Swamp Lake	YM 22365, 22370, 22381	3	"The Red-legged Frog was seen at almost every lakelet in the district. . .They were noted directly on the edges of the water, but when disturbed by us would slip into the water and remain underneath. . . They were easy to catch."	YM Collections Records, Yosemite Field School 1941	1
1944	*Rana boylii*	Yosemite Valley	OMNH 31034	1	"Merced River pond near Happy Isles."	VertNet 2020	1
1945	*Rana draytonii*	Camp Mather	AMNH 52367, 104140–104148	10		VertNet 2020	1
1950	*Rana draytonii*	Woods Creek	MVZ 50959-50962	4		VertNet 2020	1
1953	*Rana draytonii*, *Rana boylii*	Willow Creek	MVZ 59581-59587	7 collected; 3–4 more observed (*R. boylii*). *R. draytonii* "extremely abundant".	"Seven *Rana boylii* collected and three or four more seen in an hour's hunt. . .*R. aurora* [*draytonii*] was extremely abundant. An estimate of one frog per 20 feet of stream would probably be too low."	Zweifel 1953	1, 2
1954–1955	*Rana boylii*	Likely Yosemite Valley	NA	unspecified	"Occurs in small numbers along the Merced River."	Karlstrom 1962	2

APPENDIX TABLE 1. Continued.

Year	Species	Location in study area	Catalog ID/ record	N individuals	Field notes or in-text record	Source	Evidentiary standard
1954–1955	*Rana catesbeiana*	Yosemite Valley	Ahwahnee specimen may be MVZ 68054	2	"Collected one each from Stoneman and Ahwahnee meadows."	Karlstrom 1962	2
1956	*Rana catesbeiana*	Yosemite Valley	MVZ 68054	1	"Ahwahnee Reflecting Pool"	VertNet 2020	1
1958	*Rana sierrae*	Yosemite Valley	Observation ID: 3485	1	"Animal was badly deformed, blind and no muscle tone."	Yosemite Wildlife Observation Database	6
1967	*Rana draytonii*	Jordan Creek (Smith Creek area)		1	"Jordan Creek above first road crossing creek from south – approximately 2 miles north of Greeley Hill Road."	Basey 1978	1
1972	*Rana draytonii*	Piney Creek	NA	1	"The only recent record is that of H.E. Basey (personal communication) who collected *R. aurora* [*R. draytonii*] in the foothills along Piney Creek, Mariposa, Tuolumne, and Stanislaus counties in March, 1972."	Moyle 1973	3
1972	*Rana draytonii*, *Rana catesbeiana*	Piney Creek	NA	10, unspecified	"An active population was located there in 1972. . .there were about an equal number of Red-legged Frogs and Bullfrogs found along the stream at that time." "Ten *R. aurora* were observed along stream. Bullfrogs there too."	Basey 1978	2
1972, 1974	*Rana draytonii*	Piney Creek	Photograph	>1	Slide from John M. Brode, California Department of Fish and Game	Barry and Fellers 2013, Slide from John M Brode to MRJ	1
1973*	*Rana catesbeiana*	Yosemite Valley	YM 217534	1	"Near Camp 9"	YM Collections Records	1
1974–1975*	*Rana boylii*	Yosemite Valley: Indian Canyon & Pohono Bridge/ Fern Spring	NA	unspecified	"I also saw Foothill Yellow-legged Frogs—very few—in 1974 or 75 at the bottom of Indian Canyon, and Pohono Bridge/Fern Spring."	D Graber, pers. comm., 2014	2
1975*	*Rana catesbeiana*	Swamp Lake/ Miguel Meadows area	NA	unspecified	"This area was visited in the spring of 1975 and bullfrogs were abundant and no red-legged frogs were found."	Basey 1978	2
1978*	*Rana catesbeiana*	Piney Creek, Smith/Jordan Creek area	NA	unspecified	"Bullfrogs were found in the area."	Basey 1978	2

APPENDIX TABLE 1. Continued.

Year	Species	Location in study area	Catalog ID/ record	N individuals	Field notes or in-text record	Source	Evidentiary standard
1978*	*Rana catesbeiana*	Willow Creek	NA	unspecified	"This creek was visited several times and no Red-legged Frogs were found but Bullfrogs were abundant."	Basey 1978	2
1979*	*Rana catesbeiana*	Yosemite Valley	NA	unspecified	"The taking of Bullfrogs in Yosemite National Park is permissible. However, they are so few in number that I would highly recommend that you seek them elsewhere."	Keay 1979	2
1979*	*Rana catesbeiana*	Swamp Lake	NA	unspecified	"I saw lots of Bullfrogs at Swamp Lake when I went back around 1979."	D Graber, pers comm. 2014	2
1984*	*Rana draytonii*, *Rana catesbeiana*	Piney Creek	NA	1, 2	"Observed one adult RLF [California Red-legged Frog] and two large adult male Bullfrogs."	R. Hansen, pers. comm.	2
1984*	*Rana draytonii*	Smith Creek	NA	4	"Saw 2 RLF and heard 2 others jump into water (no Bullfrogs at this site)."	R. Hansen, pers. comm., 2017	2
1990	*Rana catesbeiana*	Piney Creek	CAS 178781	1	"Location searched during the day and night for California Red-legged Frogs. No frogs were found except Bullfrogs. This specimen was taken as a voucher for the surveys."	MRJ field notes, Vertnet 2020	1
1993	*Rana catesbeiana*	Piney Creek	NA	2	"1 subadult"; "1 adult"	Barry and Fellers 2013	2
1994	*Rana catesbeiana*	Piney Creek	NA	8	"3 adults; 5 subadults"	Barry and Fellers 2013	2
1997	*Rana catesbeiana*	Swamp Lake	NA	982	"18 adults, 25 subadults, 607 larvae"; "30 subadults, 300 larvae"; 2 adults	Barry and Fellers 2013	1

APPENDIX TABLE 2. Narrative historical evidence for the paucity of reliable amphibian records, lack of survey effort, and shifting management priorities in the study area.

Year	Portion of Study Area	Statement	Source
1919	Yosemite Region	"The Grinnell-era survey of frog, salamander, lizard, and snake species was haphazard at best, as species presence was recorded only when observed and no systematic survey methods were employed."	Moritz and others 2011
1924	Yosemite Region	"This species [California Red-legged Frog] is more wary than the Yellow-legged Frog and often escapes observation by reason of this fact."	Grinnell and Storer 1924
1925	Yosemite Region	"Knowledge of the local distribution of this frog is much less complete than for some of the other species of western amphibians, due to the fact that adults are quite wary, often escaping the attention of collectors, and to the further fact that the species is more active by night than by day and may not be seen unless especially hunted for after nightfall."	Storer 1925
1933	Yosemite Valley	"No other spot in a national park has as many wild-life problems of this type. Permanent residents alone number several hundred, and there are days when ten to twenty thousand people and thousands of cars are circulating in an area approximately 6 miles long by 1 mile wide between the great confining walls. They constrict the seasonal drift of game into a bottle neck. These walls tend to isolate the characteristic transition-zone fauna of the valley from any near-by source of replenishment."	Wright and others 1933
1933	Yosemite Valley	"Oil is spread on dead waters seasonally as a mosquito-abatement measure. This spells death to birds of many species that come to the quiet pools to bathe. One of the writers has picked up dozens of oil-soaked birds in the meadows, and within the space of a half hour once saw two blackbirds and a robin floating down the Merced River. Total losses from this source must be considerable."	Wright and others 1933
1938	Swamp Lake Research Reserve	"This frog [California Red-legged Frog] is much more secretive in its habits than the Sierra Yellow-legged Frog. Beyond doubt, this fact is important in its previous exclusion from amphibian check lists."	Yosemite Field School 1938
1939	Swamp Lake Research Reserve	"No intensive study of the amphibians in the research area was made."	Yosemite Field School 1939
1941	Swamp Lake Research Reserve	"It is suggested that future classes devote greater attention to changes in numbers of these animals. . .it is hoped that in future years more attention will be given to night collecting, for it is not unlikely that valuable nocturnal observations may be made regarding the life histories or occurrences of reptilian and amphibian life of the Swamp Lake area."	Yosemite Field School 1941
1946	Yosemite National Park	"Perhaps careful collecting will prove that this frog [California Red-legged Frog] is more widespread than our records thus far have seemed to indicate"	Walker 1946
1962	Yosemite Valley	"Many native western anurans with similar ecological requirements cannot compete successfully with the introduced *R. catesbeiana*, and it is to be hoped for the sake of preservation of native fauna that the Park Service officials in Yosemite can prevent this form from becoming established in the Valley."	Karlstrom 1962

APPENDIX TABLE 2. Continued.

Year	Portion of Study Area	Statement	Source
1963	Yosemite National Park	"Our aquatic ecology story is not of much interest to the average visitor, is not significant to an understanding of the park, and has serious competition from far more compelling features...since fish are a part of Yosemite's aquatic ecology story, the visitor soon loses interest in aquatic ecology in favor of the fish, concentrating his interest on what is essentially an exotic in the park."	US National Park Service 1963
1971	Yosemite Valley	"Our files do not provide enough information to determine whether or not the Bullfrog is replacing the Yellow-legged Frog in Yosemite Valley. In fact your record from Karlstrom is the first we have heard that the frogs once in the Ahwahnee Hotel Pond might have escaped."	Jones 1971
1972	Yosemite Valley	"While it is true that we have no records of recent sightings of Red-legged Frogs here [Yosemite Valley], it is also true that there hasn't been much interest in the park's reptiles and amphibians for some time. Thus, our records are probably incomplete."	Jones 1972
1972	Yosemite National Park	"If the Bullfrog's range expansion is not halted it may wipe out the native Red-legged Frog from Yosemite, as it has done throughout most of the central Sierra."	Basey 1972
1977	Yosemite National Park	"It's not often that we receive letters from people concerned with the protection of small reptiles and amphibians. . .Certainly, reptiles and amphibians play an important part in their respective niche in the ecosystem and deserve equal protection."	Wolfe 1977