

Using Demography to Evaluate Reintroductions for Conservation of the Endangered Frog, *Rana sierrae*, in Streams

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ABSTRACT: Reintroductions are an important recovery tool for endangered species but have had varying success. We used demographic data to evaluate the use of reintroductions for the recovery of the federally endangered Sierra Nevada Yellow-legged Frog (*Rana sierrae*) in stream populations in its northern range where the species is particularly at risk. We conducted a capture–mark–recapture study from 2016–2018 in four diverse streams. One of the streams contained a high abundance of frogs that allowed us to investigate demography in a relatively healthy population. In another of the streams, we tested a reintroduction using captive-reared frogs. We used robust design Huggins and Pradel models to estimate abundance, apparent overwinter survival, recruitment, longevity, and sex ratios. Annual abundance estimates were small, with ≤ 52 adult frogs at three streams and few tadpoles or subadults seen in any of the streams. The oldest frog in our streams was at least 13 yr. Estimates of apparent survival rates of wild adults ranged from 0.55 ± 0.05 standard error (SE) to 0.90 ± 0.05 SE, and estimates of annual recruitment ranged from 0.02 ± 0.11 SE to 0.26 ± 0.03 SE per site. High survival rates leading to long-lived adults may facilitate persistence of these stream populations, whereas low recruitment may limit population growth and recovery. The two largest populations were in intermittent streams, which may reflect their roles as a refuge from fishes. At least 52% of captive-reared frogs survived their first summer after release and at least 36% survived their first winter. Apparent overwinter survival of captive-reared frogs was lower than for wild frogs, ranging from 0.29 ± 0.13 SE to 0.56 ± 0.14 SE. Because of the apparent low survival of wild eggs, tadpoles, and subadults, releasing adults as was done in this study, rather than younger life stages, may be more successful. Our results offer promise for the use of reintroductions to augment depleted populations and suggest that further research on factors affecting recruitment and survival of younger life stages is needed.

Key words: Amphibian; Captive-rearing; Endangered species; Mark–recapture; Population augmentation; Sierra Nevada Yellow-legged Frogs

REINTRODUCTIONS are increasingly used as a recovery tool for endangered species (Bar-David et al. 2005; Hunter et al. 2010; Forstner and Crump 2011; Miskelly and Powlesland 2013; Tuberville et al. 2019). We define reintroductions broadly to include the release of translocated or captive-reared individuals to augment existing populations (Hunter et al. 1999; Bertolero et al. 2007; Hunter 2007), to re-establish populations in habitats where the species is locally extinct (Denton et al. 1997; Tavecchia et al. 2009), and to establish new populations in areas where the species either did not occur or its prior status is unknown (Denton et al. 1997; Bell et al. 2004). The success of reintroductions has varied resulting from factors that range from existing environmental conditions at release sites to the design of release programs (Dodd and Seigel 1991; Bloxam and Tonge 1995; Fischer and Lindenmayer 2000; Germano and Bishop 2009). Existing conditions include habitat quality and the presence of threats (Germano and Bishop 2009; Joseph and Knapp 2018). Designs of release programs include criteria such as life stages, number of animals, and number of batches released (Reynolds et al. 2013; Rummel et al. 2016). As a result, there is a growing awareness of the need to first evaluate whether a reintroduction may succeed and is the best choice for a given conservation challenge and, second, to evaluate the best design for an effective release program

(Dodd and Seigel 1991; Denton et al. 1997; Fischer and Lindenmayer 2000; Armstrong and Seddon 2008; Germano and Bishop 2009). Small-scale or pilot reintroductions can be pivotal to avoiding costly mistakes before full implementation in conservation programs.

Demographic information about a species is paramount for developing an effective reintroduction program (Bell et al. 2004; Bar-David et al. 2005; Cayuela et al. 2019). Knowledge of a species demography guides reasonable expectations for the outcome of a reintroduction (Seddon et al. 2007) and aids in designing a more successful program (Tocher et al. 2006; Collazo et al. 2013; Reynolds et al. 2013). Developing reasonable expectations requires understanding the biological constraints of a species such as typical abundances, survival rates, and potential for population growth (Dodd and Siegel 1991; Cayuela et al. 2019; Honeycutt et al. 2019). Designs of reintroduction programs ideally incorporate species-specific data on age structure, survival of different life stages, sex ratios, and reproductive potential (Dodd and Siegel 1991; Biek et al. 2002; Hunter 2007; Muths et al. 2014). Quantitative information on these demographic parameters provides insights into which life stages to release (Muths et al. 2014; Cayuela et al. 2019), whether sex ratios affect population establishment (Dodd and Siegel 1991), and the best configurations of numbers of individuals, frequency, and timing of releases (Tocher et al. 2006; Germano and Bishop 2009; Collazo et al. 2013; Reynolds et al. 2013). Finally, demographic data can inform

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decisions that increase chances of successful reintroductions while minimizing impacts to source populations caused by the collection of animals (Tocher et al. 2006).

Reintroductions, including the use of captive-reared animals, are being considered as a potential conservation action for Sierra Nevada Yellow-legged Frogs (*Rana sierrae*; Mountain Yellow-legged Frog Interagency Technical Team [MYLF ITT] 2018). Once considered one of the most abundant and widespread amphibians in the Sierra Nevada Mountains of California, USA (Grinnell and Storer 1924; Wright and Wright 1949), the endemic *R. sierrae* is now a federally listed endangered species (US Fish and Wildlife Service [USFWS] 2014). Estimates of range-wide declines of *R. sierrae* and the closely related *Rana muscosa* indicate disappearances from more than 90% of historical localities (Vredenburg et al. 2007) and about 50% of watersheds where reproduction had been documented prior to 1990 (Brown et al. 2014a). Primary causes of range-wide declines include the introduction of nonnative fishes to formerly fishless habitats (Knapp and Matthews 2000; Vredenburg 2004; Knapp 2005) and the amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*), which is responsible for amphibian declines worldwide (Rachowicz et al. 2006; Scheele et al. 2019). Given the small size and isolation of many remaining populations, recovery of *R. sierrae* will likely require reintroductions (Joseph and Knapp 2018; MYLF ITT 2018).

The demography of *R. sierrae* has primarily been studied in the context of understanding threats and recovery actions (Vredenburg 2004; Briggs et al. 2010; Joseph and Knapp 2018), though a few studies provide baseline vital rates (Fellers et al. 2013; Brown et al. 2019). These studies suggest reintroductions may be a viable recovery tool, at least in alpine lakes where the species has been most studied. In lakes, *R. sierrae* and the closely related *R. muscosa* have the potential for rapid recovery if the causes of declines are removed. In the absence of other threats, for example, removal of introduced fish predators from lakes has led to rapid increases in frog abundances (Vredenburg 2004; Knapp et al. 2007). However, if the causes of decline remain, reintroductions may not be successful (Dodd and Seigel 1991; Fischer and Lindenmayer 2000). Experimental reintroductions of these frogs in high elevation mountain lakes containing *Bd*, for example, have had mixed success (Fellers et al. 2007; Joseph and Knapp 2018).

Rana sierrae is particularly at risk in its northern range where the few remaining populations have low abundances (Brown et al. 2014b, 2019; MYLF ITT 2018). Populations in the northern range also commonly occur in streams, a habitat type where the species is much less studied. The lack of knowledge of the ecology of these northern stream populations has limited the ability to evaluate restoration options, including reintroductions. There are little historical or demographic data, and population monitoring in four streams has found low abundances of <15 adult frogs (Brown et al. 2019). Further, very little is known about the breeding ecology and recruitment of *R. sierrae* in northern streams. Although tadpoles and subadults are occasionally found in these streams, there are only a few known breeding areas that are located in shallow in- and off-channel habitats (Brown et al. 2019). These habitats are very different from the 4–5-m depths assumed to be required based on lake

studies (Bradford 1983; Knapp et al. 2003; Knapp 2005). Thus, further information on the demography and breeding ecology of stream populations in the northern Sierra is needed to evaluate the efficacy of reintroductions as a recovery tool (MYLF ITT 2018).

We quantified the demography of *R. sierrae* in four diverse northern Sierra Nevada streams and pilot-tested population augmentation in one of the streams. Our objectives were to: (1) quantify changes in abundance and survival and estimate other vital rates in three at-risk stream populations first monitored 4 yr earlier; (2) quantify abundance and vital rates in a larger, presumably healthy, stream population and in two additional headwater creeks; (3) increase our knowledge of *R. sierrae* breeding ecology and recruitment in streams; and (4) pilot-test a population augmentation form of reintroduction. Results from this study will provide valuable baseline information to evaluate whether reintroductions are a feasible recovery tool for *R. sierrae* in northern streams and, if so, how best to design a reintroduction program.

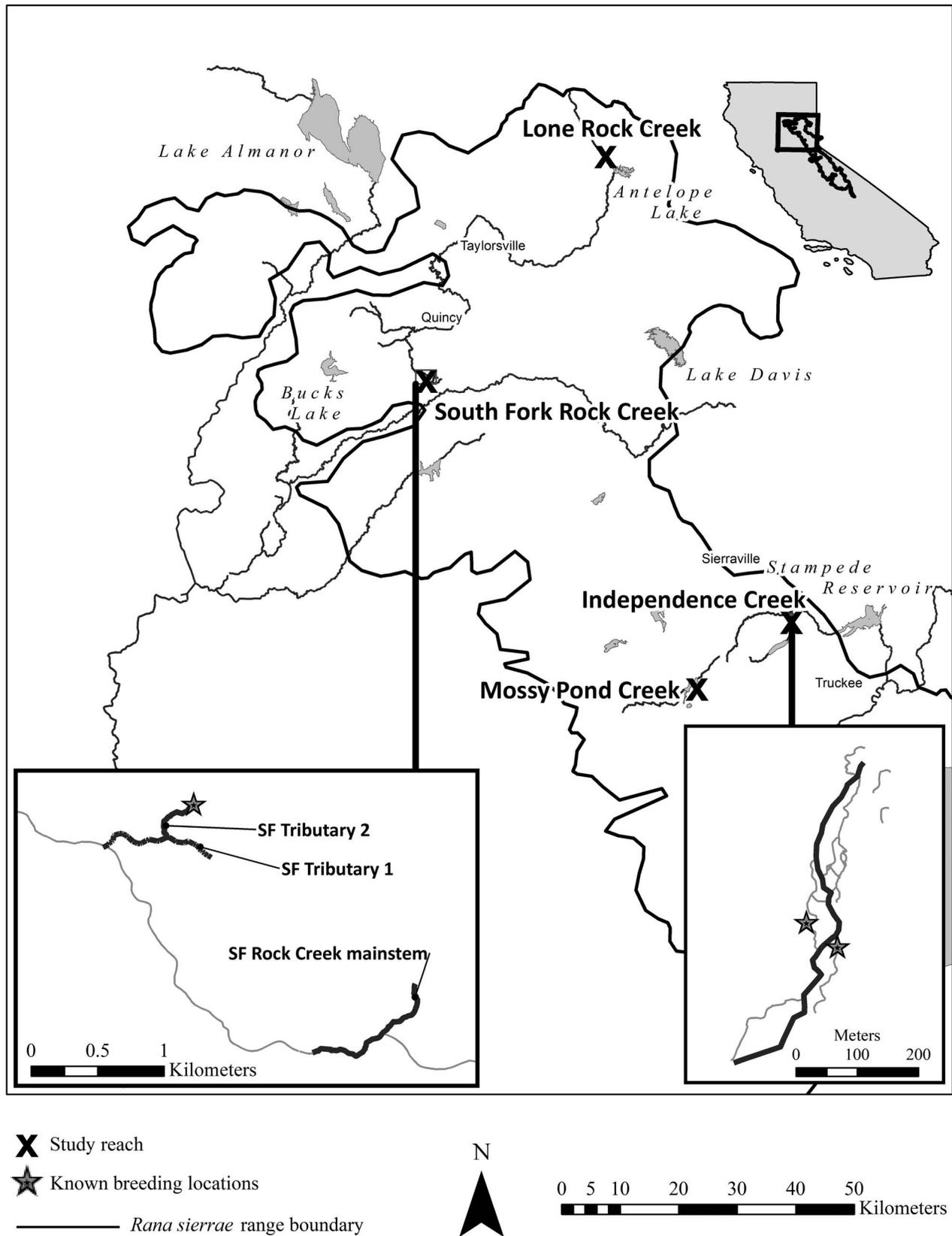
MATERIALS AND METHODS

Study Streams

We selected four streams across the northern range of *R. sierrae* known to be occupied by the species and that varied by size, geomorphology, hydrology, and population abundance (Fig. 1). Three of the streams had been monitored from 2009–2011 (Brown et al. 2019) and were included in this study to assess demographic changes over the intervening period. We added Mossy Pond Creek to provide demographic data for a presumed healthy population.

The two perennial stream reaches, Independence Creek (1966 m elevation, 0.66 km length) and Lone Rock Creek (1547 m elevation, 2.7 km length), are low to moderate gradient, second and third order reaches associated with reservoirs. Independence Creek is fairly uniform and dominated by riffles and pools. Flows at Independence Creek are regulated by an upstream reservoir that is located on a preserve. This reach flows through a meadow with multiple braided side channels, floodplains, and off-channel habitats. The total length of the side channels is greater than the length of the main channel. This mosaic of wet habitats outside the main channel is inundated at snowmelt, generally dry by midsummer, and may reappear in the fall from water releases from the upstream dam. *Rana sierrae* breeds in two intermittent side channels of Independence Creek that have sections retaining water all summer. Lone Rock Creek, in contrast, flows through open forest, has a deeper channel valley, is relatively down cut with large sections of eroded banks, and flows into a large reservoir popular with recreationists and anglers. This more diverse stream is dominated by long deep pools and runs interspersed with higher gradient cascades and low-gradient riffles. Prior surveys found *R. sierrae* populations to be small in both Independence Creek and Lone Rock Creek (<15 adults; Brown et al. 2019). Native and nonnative fishes were present in Independence Creek and abundant in Lone Rock Creek.

The two intermittent streams, South Fork (SF) Rock Creek and Mossy Pond Creek, are small, high-gradient headwater creeks with large sections that dry, typically by midsummer. Frogs concentrate around the remaining pools.



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FIG. 1.—Locations of *Rana sierrae* streams surveyed 2016–2018. Insets show breeding areas.

SF Rock Creek consists of three reaches: the headwaters of the main channel (1651 m elevation, 1.0 km length) and two tributaries, SF Tributary 1 (1425 m elevation, 1.2 km length) and SF Tributary 2 (1487 m elevation, 0.4 km length; Fig. 1). The three reaches are connected by water in the spring but become disconnected as water dries. These reaches are dominated by medium-gradient cascades and pools. The intermittent water limits fishes from persisting in the SF Rock Creek reaches, though they are occasionally found in the main channel and lower sections of SF Tributary 1. Prior surveys in the SF Rock Creek main channel found very small numbers of frogs (<5 adults; Brown et al. 2019), only a few frogs had been found in SF Tributary 1 during limited surveys, and the SF Tributary 2 population was a new discovery during this study. Mossy Pond Creek (2034 m elevation, 0.9 km length) flows from a shallow lake into a reservoir and is surrounded by granitic bedrock. Chute, cascade, and pool geomorphology dominates this stream. A steep barrier at the confluence with the reservoir prevents fishes from entering Mossy Pond Creek, including the headwater lake. Preliminary surveys of Mossy Pond Creek found a relatively large number of frogs (California Department of Fish and Wildlife unpublished data).

Mark–Recapture Surveys

We conducted capture–mark–recapture surveys from 2016–2018 using a robust design (Pollock 1982). The robust design has two tiers that include primary sampling periods over longer intervals that allow population gains (recruitment/immigration) and losses (mortality/emigration) and secondary sampling occasions within each primary period where the population is assumed to be closed. In each year (primary period), we surveyed each of the four streams four times (secondary occasions) approximately monthly, from early summer (June) into fall (September to mid-October). Annual precipitation varied among years; snowpacks on 1 April were 94% of normal for 2016, 148% of normal in 2017, and 46% of normal in 2018 (California Department of Water Resources; <http://cdec.water.ca.gov/snowapp/sweq.action>). High spring flows in 2017 limited early season surveys of the Independence Creek main channel and several side channels as well as sections of Lone Rock Creek. During the 2017 high flows at Independence Creek, we found frogs in the mosaic of off-channel aquatic habitats. For each secondary occasion, we walked the entire reach length at least twice, usually over multiple days, conducting surveys after 0930 h to maximize detection and starting in different locations each pass to minimize detection bias related to time of day.

We surveyed all wadable water including stream channels, mouths of tributaries, side channels, backwaters, and nearby floodplains. We caught frogs by hand or with a hand net. We recorded sex, weight, length (snout–urostyle length [SUL]), and a unique passive integrated transponder (PIT) tag number for each captured frog. We PIT-tagged all newly captured adults ≥ 45 mm SUL using Avid MUSICC PIT tags or, in some cases, ≥ 40 mm SUL using BioMark Microchips™ (Biomark, Inc.). We considered frogs ≥ 40 mm to be adults (Matthews and Miaud 2007; Fellers et al. 2013). We counted frogs too small to mark and tadpoles individually when possible, or rounded to the nearest 10 for numbers up to 100 and to the nearest 100 for numbers greater than 100.

We visually estimated the number of fishes using the same approach.

Captive-Rearing and Frog Release

Prior to this study, the only known breeding sites in these streams were on Independence Creek. On 26 May 2016, Plumas National Forest crews found a small (~ 25 m²) breeding pool with several hundred tadpoles just off the main channel at SF Tributary 2 (Fig. 1). On 27 May 2016, we collected 105 tadpoles from this pool plus a few other locations on the SF Rock Creek tributaries and transported them to the San Francisco Zoo and Gardens following protocols specified in the Interagency Mountain Yellow-legged Frog Conservation Strategy (MYLF ITT 2018). Of these 105 tadpoles, 90 died within a few weeks due to an error in the installation of a new water filtration system that allowed entry of chlorine over several days before it was discovered and repaired. The tadpoles that were only a few weeks old were especially susceptible to the low levels of chlorine in their environment. In October 2016, we collected an additional 80 older tadpoles from the same pool and transported them to the San Francisco Zoo. The life-support system was fixed and 92 of the remaining 95 tadpoles survived to adulthood.

We reared the tadpoles through metamorphosis at the San Francisco Zoo following strict quarantine holding (Poole and Grow 2012). We kept frogs and tadpoles in large water volumes in enclosures constructed of glass for easy disinfection and with screened lids to prevent frogs from escaping. Water depth was 25–30 cm for swimming larvae and 15–30 cm for metamorphosing larvae and small frogs. Enclosures included hiding spots, basking logs, and aquatic perches. Ambient temperatures were 10–18°C with a specific hot spot of 29–32°C to provide a thermal gradient. Water temperature was between 10–18°C with seasonal changes to mimic natural temperatures. Compact fluorescent lights on a timer simulated natural sunlight at levels approximating wild habitat. Mercury vapor ultraviolet B (UV) lamps provided ultraviolet B (UVB) lighting.

We used filtration in conjunction with UV sterilizers to reduce the density of aquatic bacteria and parasites and maintain stable water quality. To reduce buildup of organic waste, we changed 25–50% of the water in the tanks twice weekly with reconstituted reverse osmosis water. We tested water quality weekly for frogs and daily for tadpoles. We maintained water quality at near-neutral pH and very low conductivity based on other successful collection locations that were typically granitic basins in the central and southern Sierra Nevada.

Tadpoles were offered food twice daily using Spirulina-based fish foods including an algae gel (Repashy Superfoods Soilent Green meal replacement gel; Repashy Ventures Inc.) and a reconstituted powdered feed plated for grazing (sera Micron Nature; sera Ltd.). Frogs were fed daily for the first year and then three times per week with a variety of invertebrates including domestic crickets, mealworm larvae, mealworm adult beetles, flightless houseflies, flightless fruit flies, and wax worm larvae. Feeder insects were gut loaded and dusted with calcium with D₃ and multivitamin. Food was offered alive to elicit and reinforce natural foraging behaviors. To maintain innate antipredation behaviors, staff handled frogs only during necessary health examinations. In

total, 92 tadpoles were reared to the adult stage. We know wild tadpoles in the SF Rock Creek reaches overwinter at least once, and subadults probably take at least 2 yr to mature. In the controlled conditions in the zoo, all tadpoles developed into adults within 2 yr.

All frogs released to the wild in 2017 and two thirds of the frogs released in 2018 were exposed to *Bd* in the zoo and subsequently cleared with the antifungal drug itraconazole prior to release in an effort to stimulate their immune system to recognize *Bd* (Garner et al. 2008; Jones et al. 2012). One third of the 2018 release was left untreated as a control. Prior to release, we marked all frogs with a PIT tag and clipped the tip of the outer toe on the front foot as a year batch mark.

On 18 July 2017, we released 22 frogs into their natal watershed, SF Rock Creek. We released the frogs into two pools on each of the two SF Rock Creek tributaries, divided evenly among the pools. We chose the four pools based on water presence into mid-October and frog presence in 2016. On 5 July 2018, we released 60 frogs into the two SF Rock Creek tributaries plus the main channel. We selected pools using the same criteria as in 2017 and included the 2017 release pools. We released 20 frogs into each reach divided equally among three pools on the main channel and SF Tributary 1 and two pools on SF Tributary 2. We assigned frogs to each pool using a balanced design incorporating *Bd* exposure and sex. In both years, we monitored the released frogs during the 2 d immediately following release and subsequently during population surveys over the remaining season. We documented a few mortality events using radio telemetry data.

In 2018, to investigate the effect of the *Bd* exposure and the role *Bd* may play in the survival of the captive-reared frogs, we collected skin swabs from all captured frogs (wild and captive-reared) in the SF Rock Creek reaches using standard protocols (Hyatt et al. 2007; Vredenburg et al. 2010; Joseph and Knapp 2018). We analyzed skin swabs using standard *Bd* DNA extraction and quantitative polymerase chain reaction (qPCR) methods (Boyle et al. 2004; Kriger et al. 2006; Vredenburg et al. 2010; Joseph and Knapp 2018).

Data Analysis

For the four study streams, we used the Huggins and Pradel forms of Pollock's robust design (Pollock 1982) to estimate abundance, apparent overwinter survival, and recruitment of adults for each stream, year, and sex and to compare the apparent survival of captive-reared frogs released in 2017 to 2018 with that of wild adults. For both forms of the model, we assumed the probability of capture (p) was constant across secondary occasions (model M_{01} ; White et al. 1982). The robust design assumes population closure across secondary occasions (summer in our case), meaning there is no recruitment into or loss of individuals (through movement or birth/death) from the study population. Violations of this assumption would lead to underestimates in p , which would lead to overestimates in population size. Abundance estimates would be unbiased if such inputs or outputs to the study population were random (Kendall 1999). There were no indications of nonrandom inputs or outputs to our stream populations and, as a double-check, we ran a simple Cormack–Jolly–Seber model to estimate monthly summer survival. This resulted in a survival estimate

of 0.85 ± 0.01 SE for the summer, indicating the populations were largely closed over the study period.

We used Huggins robust design to estimate abundance and apparent survival. We compared all combinations of additive models where apparent survival (Φ) and the probability of capture (p) were either held constant or allowed to vary among streams, years, sex, and captive-reared versus wild frogs. Although temporary emigration may have occurred at our streams, models were not able to estimate this parameter because of the low numbers of frogs and short duration of our study (3 yr). Thus, we fixed temporary emigration to 0. We compared models using Akaike Information Criterion adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002). All models converged, and final estimates were calculated by model averaging. We report the models comprising the top 95% cumulative weight in the model set for each run.

We used Pradel robust design models (Pradel 1996; Schueller and Peterson 2010; Pederson et al. 2012) to estimate recruitment for wild frogs. We chose the Pradel formulation that estimates recruitment and survival. We used the probability of capture (p) structure from the parsimonious models ($\Delta AIC_c < 2$) of the Huggins robust design (stream and year) with the omission of sex and captive-reared versus wild frogs. We omitted sex to simplify the models, given our small sample sizes, and because model averages of probability of capture from the Huggins models were essentially the same between the sexes (differences ≤ 0.05 with similar confidence intervals; see Supplemental Materials). We excluded captive-reared frogs because their recruitment was a given. We compared all combinations of additive models where recruitment rate (f) and survival (Φ) were held constant or allowed to vary among streams and years. Similar to the Huggins analyses, we compared models using AIC_c and calculated final estimates by model averaging (Burnham and Anderson 2002). Model fitting and averaging were conducted using the R (v3.5.2–3.6.1; R Core Team 2018) package RMARK (Laake 2013). Other data processing and analysis were conducted using SAS v9.4 (SAS Institute Inc., Cary, NC).

For unmarked subadult and tadpole stages, we reported the maximum number of individuals found on a given day. Because so few frogs were infected with *Bd*, we descriptively summarized frequencies of infection. We calculated sex ratios for each stream using the capture–mark–recapture abundance estimates and tested for biased sex ratios using the normal approximation to the binomial test (Kachigan 1986). We reported known mortality events of radio-tracked frogs.

We included data from prior monitoring (Brown et al. 2019) to examine longevity of adults. We estimated longevity using adults first captured 2009–2011 from the three streams where surveys spanned 10 yr (Lone Rock Creek, Independence Creek, SF Rock Creek main channel) plus adults first captured in 2013 Independence Creek surveys. We reported the number of years from first to last capture because we do not know the length of the tadpole and subadult stages. For the last capture, we used all available data including surveys from 2009–2011, 2013 in Independence Creek, 2015 in Lone Rock Creek and SF Rock Creek main channel, and 2016–2018. We know tadpoles in our streams overwinter at least once (Brown et al. 2019), and subadults probably take at

least 2 yr to mature. Thus, we assumed a conservative 14–16-month tadpole and 2-yr subadult stage, making our age estimates conservative minimums that are at least 3 yr less than the true age.

RESULTS

Demography of Adult Wild Frogs

Overall, abundances of wild frogs were low, with larger numbers of frogs in the intermittent creeks than in the perennial streams (Table 1). The number of unique individuals found per stream was 19 in both Lone Rock and Independence Creeks, 9 in the SF Rock Creek main channel, 51 in the two SF Rock Creek tributaries combined, and 227 in Mossy Pond Creek. Model abundance estimates were similar to the counts.

Four of the Huggins robust design models had equal support with $\Delta AIC < 2$ and relatively equal weights summing to 0.92 (Table 2). The remaining models differed in rank by more than four AIC each, with weights < 0.03 . Probability of capture varied by stream, year, sex, and captive-reared versus wild frogs. In the parsimonious models, apparent survival varied by stream and captive-reared versus wild frogs, and there was some support for differences among sexes and years. Two of the Pradel robust design models had equal support with $\Delta AIC < 2$ summing to 0.68 of the weight (Table 2). In the parsimonious Pradel models, apparent survival varied by stream with some support for differences among years. Recruitment varied by stream. Probability of capture was essentially the same for both Huggins and Pradel models and ranged from 0.21 ± 0.05 SE to 0.66 ± 0.02 SE (see Supplemental Materials).

Annual abundance estimates of wild frogs from the Huggins models were < 30 adults at all reaches except Mossy Pond Creek. The smallest annual abundance estimate was in the main channel of SF Rock Creek with a maximum of 3.4 ± 0.7 SE females and 4.8 ± 1.0 SE males in 2017. The two SF Rock Creek tributaries combined had larger numbers of frogs compared with Independence Creek, Lone Rock Creek, and the SF Rock Creek main channel. The two tributaries were in close proximity, were connected hydrologically, and frogs occasionally moved between them; a long stretch of seasonally dry streambed separated the SF Rock Creek main channel reach from the mouth of SF Tributary 1, and no frogs were documented moving between these reaches. Mossy Pond Creek had the most frogs, as expected. Average densities in Mossy Pond Creek were 47.0 to 144.6 frogs/100 m wetted stream length greater than the perennial streams. Average densities in the SF Rock Creek tributaries were 4.1 to 18.9 frogs/100 m wetted stream length greater than the perennial streams.

Apparent survival of adults from the Huggins models was consistent among years and varied among the streams, with no pattern between perennial and intermittent streams (Table 1). Apparent survival was relatively low at Lone Rock Creek (e.g., females = 0.56 ± 0.13 SE) and Mossy Pond Creek (e.g., females = 0.55 ± 0.05 SE) and greater at Independence Creek (e.g., females = 0.83 ± 0.09 SE) and the three SF Rock Creek reaches (e.g., females at SF Tributary 1 = 0.89 ± 0.05 SE). One frog was eaten by a Sierra Gartersnake (*Thamnophis couchii*) on SF Tributary 2

and one was eaten by a Gartersnake of unknown species (*Thamnophis* spp.) on Mossy Pond Creek.

Annual recruitment estimates from the Pradel models over the 3-yr period were low, with a maximum of 0.26 ± 0.03 SE at Mossy Pond Creek (Table 1). However, over a longer period, new frogs were added to the populations. In the three streams with prior monitoring data, the majority of adults found during this study (2016–2018) had not been found during the previous surveys (Lone Rock Creek = 91%, Independence Creek = 63%, SF Rock Creek main channel = 83%).

With a few exceptions, sex ratios were close to 1:1 (P from binomial test range = 0.18–0.98; Table 3). At Independence Creek, more females were found in 2016 ($P = 0.09$) and more males in 2018 ($P = 0.04$). The numbers of estimated individuals were too low for the binomial test for Lone Rock Creek in 2017, SF Rock Creek main channel in all years, and SF Tributary 2 in 2018. At Lone Rock Creek in 2017, an estimated 4.2 females and no males were found.

A total of 38 individual adult frogs were first captured 2009–2013 in the three streams with surveys spanning 10 yr (excluding Mossy Pond Creek and the two SF Rock Creek tributaries). One male on the SF Rock Creek main channel was caught 10 yr apart (first caught 2009, last caught 2018), making it a minimum of 13 yr old (Fig. 2). Four frogs were caught 9 yr apart and 5 frogs, 8 yr apart. Of the 14 frogs found at least 5 yr apart, eight were from Independence Creek. Ages appeared equal between the sexes.

Reproduction

We distinguished breeding areas as locations where there were larger numbers of tadpoles clustered in one location relative to locations with a few scattered tadpoles, which we sometimes found. We found tadpoles in previously known and new breeding areas. We found tadpoles each year in the two side channels at Independence Creek where breeding was previously known to occur. In spring 2016, we found the two breeding pools at the upper end of SF Tributary 2. These SF Tributary 2 pools were hydrologically connected to the main channel during snowmelt, but disconnected most of the summer. One of the pools dried each year, stranding tadpoles, and the other pool was spring-fed and retained water all summer. In 2018, breeding areas were found in three new locations: the upper part of the SF Rock Creek main channel and in two pools on SF Tributary 1. Each year we found a few tadpoles scattered in additional locations on the SF Rock Creek tributaries, Mossy Pond Creek, and Lone Rock Creek.

Overall, we found few of the younger life stages in any of the stream reaches (Table 4). In the known breeding areas, we reliably found tadpoles each year, but numbers were small with maximum counts on a given day ranging from 18–158 at Independence Creek and 18–525 at SF Tributary 2. Egg masses generally have 100–300 eggs, so 525 tadpoles may come from only a few masses. The maximum counts of subadults per day were also very small. The most subadults found was at Mossy Pond Creek, with numbers that ranged from only 11–26 individuals.

There were indications at several streams that 2018 was a relatively good year for breeding compared with prior years (Table 4). We found larger numbers of tadpoles in the known breeding areas as well as the discovery of the three

TABLE 1.—Demographic parameter estimates for wild *Rana sierrae* in four northern Sierra Nevada streams surveyed 2016–2018. The top half shows counts of unique individuals. The bottom half shows model estimates. Abundance and survival estimates are model averages from Huggins robust design models. Recruitment estimates are model averages from Pradel robust design models. Est = estimate; SE = standard error; CI = confidence interval. Lone Rock Creek and Independence Creek are perennial streams; the others are intermittent streams.

	Lone Rock Creek			Independence Creek			Mossy Pond Creek			South Fork Rock Creek Main Channel			South Fork Rock Creek Tributary 1			South Fork Rock Creek Tributary 2		
	Est.	SE	CI	Est.	SE	CI	Est.	SE	CI	Est.	SE	CI	Est.	SE	CI	Est.	SE	CI
Count of unique individuals 2016–2018																		
Female	11			9			118			5			14			9		
Male	8			10			109			4			17			11		
	Lone Rock Creek			Independence Creek			Mossy Pond Creek			South Fork Rock Creek Main Channel			South Fork Rock Creek Tributary 1			South Fork Rock Creek Tributary 2		
Abundance																		
Female																		
2016	9.1	2.5	6.8–18.3	11.6	2.6	9.0–20.8	70.5	3.0	66.7–79.5	3.6	0.8	3.1–7.8	15.3	2.2	13.0–22.9	6.3	1.3	5.2–11.9
2017	4.2	1.4	3.2–10.4	9.5	2.0	7.6–17.1	63.4	2.4	60.6–70.9	3.4	0.7	3.0–7.2	10.9	1.6	9.5–17.0	6.0	1.1	5.2–11.0
2018	6.7	1.0	6.1–11.4	3.3	0.6	3.0–6.6	59.8	0.9	59.1–63.9	4.1	0.4	4.0–6.4	11.6	0.8	11.1–15.4	5.2	0.5	5.0–8.1
Male																		
2016	10.0	3.0	7.1–20.6	4.7	1.7	3.3–11.9	73.2	3.7	68.2–83.7	2.5	0.8	2.1–6.7	12.2	2.3	9.9–20.1	12.1	2.2	9.9–20.0
2017	0.0			11.7	2.6	9.1–20.9	63.1	2.9	59.5–71.7	4.8	1.0	4.1–9.5	14.1	2.1	11.9–21.5	10.1	1.8	8.5–16.8
2018	4.7	1.0	4.1–9.3	11.4	1.4	10.3–17.2	56.2	1.1	55.2–60.8	3.1	0.4	3.0–5.5	12.9	1.0	12.2–17.4	4.3	0.6	4.0–7.4
Survival ¹																		
Female																		
17–18	0.56	0.13	0.31–0.77	0.83	0.09	0.59–0.95	0.55	0.05	0.46–0.64	0.86	0.11	0.51–0.97	0.89	0.05	0.75–0.96	0.74	0.09	0.53–0.88
Male																		
17–18	0.58	0.13	0.33–0.79	0.85	0.08	0.61–0.95	0.57	0.05	0.48–0.66	0.87	0.10	0.53–0.97	0.90	0.05	0.76–0.96	0.76	0.09	0.55–0.89
Recruitment	0.19	0.09	0.07–0.41	0.02	0.11	0.0–1.0	0.26	0.03	0.20–0.32	0.15	0.12	0.03–0.53	0.09	0.07	0.02–0.33	0.11	0.07	0.03–0.33

¹ Survival was similar for both years so only data for 2017–2018 are shown.

new areas. For the first time in 6 yr of surveys, we found evidence that at least one egg mass had been laid in the SF Rock Creek main channel. In addition, for the first time in this reach, three older tadpoles with legs were found in the spring, indicating that breeding had occurred in prior years. Recently metamorphosed individuals were found about a month later, and then small subadults, possibly the same individuals, were occasionally found during the summer. One of the new areas with tadpoles on SF Tributary 1 was a pool where captive-reared frogs had been released in 2017. Finally, a maximum count of 23 subadults was found on Lone Rock Creek compared with only four during the prior 2 yr.

Population Augmentation of Captive-Reared Frogs

Of the 82 captive-reared frogs released into the SF Rock Creek reaches in 2017 and 2018, 52% were known to be alive at the last survey of 2018, 13% were last found midsummer

of their release year, 7% were known or presumed mortalities, and 27% were never seen after their release period (Fig. 3). At least eight of the 22 frogs released in 2017 survived to 2018. For two of these frogs, the 2018 sighting was the first time they were seen after their release period. From the Huggins models, the estimated apparent survival of captive-reared frogs from 2017 to 2018 was lower than for wild frogs and ranged from 0.29 ± 0.13 SE to 0.56 ± 0.14 SE, with no difference between the sexes (Table 5). Three confirmed mortalities of captive-reared frogs occurred in 2017, two to *T. couchii* predation and one from unknown causes. We were not able to model within-summer survival with our design, so we examined observed numbers. Based on counts, survival may have been higher in 2017, with at least 63% of 22 released frogs surviving to the end of the season compared with 48% of 60 frogs in 2018. More than twice as many frogs were found alive at the end of 2018 in

TABLE 2.—Huggins and Pradel robust design model selection for demographic parameter estimates for *Rana sierrae* in four northern Sierra Nevada streams surveyed 2016–2018. K is the number of parameters in the model. AICc is the Akaike Information Criterion adjusted for small sample sizes. Δ AICc is the difference in AIC value from the parsimonious model. w_i is the Akaike weight for comparing models. Φ is apparent survival. f is recruitment. p is probability of capture. Only top models with cumulative weight of 95% are shown.

Model	K	Deviance	AICc	Δ AICc	w_i
Huggins robust design					
Φ (stream + wild/zoo), p (stream + year + sex + wild/zoo)	19	4505.8	3888.9	0.00	0.35
Φ (stream + year + wild/zoo), p (stream + year + sex + wild/zoo)	20	4504.6	3889.8	0.90	0.22
Φ (stream + sex + wild/zoo), p (stream + year + sex + wild/zoo)	20	4504.7	3889.9	0.99	0.21
Φ (stream + year + sex + wild/zoo), p (stream + year + sex + wild/zoo)	21	4503.5	3890.7	1.87	0.14
Φ (stream + wild/zoo), p (stream + year + wild/zoo)	17	4515.1	3894.0	5.17	0.03
Pradel robust design					
Φ (stream), f (stream), p (stream + year)	20	1595.3	4006.5	0.00	0.44
Φ (stream + year), f (stream), p (stream + year)	21	1594.5	4007.8	1.27	0.24
Φ (stream), f (stream + year), p (stream + year)	21	1595.3	4008.6	2.08	0.16
Φ (stream + year), f (stream + year), p (stream + year)	22	1594.5	4009.9	3.35	0.08
Φ (stream), f (.), p (stream + year)	15	1610.5	4011.3	4.84	0.04

TABLE 3.—Sex ratios (female:male) for wild *Rana sierrae* in four northern Sierra Nevada streams surveyed 2016–2018. Sex ratios are based on abundance estimates, *P*-values test for biased sex ratio, and confidence intervals (CI) show proportion of females. Lone Rock Creek and Independence Creek are perennial streams; the others are intermittent streams. Numbers of estimated individuals were too low for the binomial test for Lone Rock Creek in 2017, SF Rock Creek main channel all years, and SF Tributary 2 in 2018. No males were found at Lone Rock Creek in 2017.

Year	Lone Rock Creek			Independence Creek			Mossy Pond Creek			South Fork Rock Creek Main Channel			South Fork Rock Creek Tributary 1			South Fork Rock Creek Tributary 2		
	Ratio	<i>P</i>	CI	Ratio	<i>P</i>	CI	Ratio	<i>P</i>	CI	Ratio	<i>P</i>	CI	Ratio	<i>P</i>	CI	Ratio	<i>P</i>	CI
2016	0.9:1	0.84	0.36–0.59	2.5:1	0.09	0.60–0.82	1.0:1	0.82	0.45–0.53	1.4:1		0.39–0.79	1.3:1	0.55	0.46–0.65	0.5:1	0.18	0.23–0.45
2017	4.2:1			0.8:1	0.63	0.34–0.56	1.0:1	0.98	0.46–0.55	0.7:1		0.24–0.59	0.8:1	0.52	0.34–0.54	0.6:1	0.31	0.25–0.49
2018	1.4:1	0.55	0.44–0.73	0.3:1	0.03	0.12–0.33	1.1:1	0.74	0.47–0.56	1.3:1		0.38–0.75	0.9:1	0.79	0.37–0.57	1.2:1		0.39–0.71

the SF Rock Creek main channel and SF Tributary 1 than in SF Tributary 2 (Fig. 3).

Infection by *Bd* and Fish

Data from the *Bd* exposure in the zoo suggested different susceptibility to infection than did data from skin swabs collected from frogs in the field. In the zoo, our captive-reared frogs seemed particularly susceptible to *Bd* infection compared with captive-reared frogs collected from other locations in the Sierra Nevada. Our frogs became infected quickly after exposure to *Bd* and, in 2018, eight (17%) died during immunization even though we reduced the exposure period by a third of the time. In contrast, we found very little infection in the field. After the release in 2018, we collected 257 *Bd* swabs from wild and captive-reared frogs in the SF Rock reaches, including 93 adults and 13 subadults. Only eight adult frogs tested positive for *Bd* and the levels of infection in all eight individuals were low (median = 260, range = 18–8722 internal transcribed spacer 1 [ITS1] copies per swab). These levels of infection are much lower than the 600,000 ITS1 copies per swab (=10,000 zoospore equivalents) that are associated with severe disease (Vredenburg et al. 2010; see Joseph and Knapp 2018 for details on the

conversion between zoospore equivalents and ITS1 copies). Of the eight infected frogs, five were wild and three were captive-reared. All five wild frogs were from the two SF Rock Creek tributaries, and one infected zoo frog was found on each of the three reaches. Our sample size was very low, but based on these raw data, there were no patterns of infection among release locations, sexes, or *Bd* exposure. All three infected captive-reared frogs were exposed to *Bd* in the zoo prior to their release and none of the control frogs tested positive. All but one of the eight infected frogs were captured more than once, and all but one infection was found in late-August to mid-October. The two frogs with the lowest *Bd* loads (<20 ITS1 copies per swab) were found again 2 wk later with no infection.

Maximum counts of fish per day at Lone Rock Creek were >450 trout in all three years, 82 Sacramento Suckers (*Catostomus occidentalis*) in 2017, and 372 Sacramento Suckers in 2018. At Independence Creek, maximum counts per day were 501 trout in 2016, 50 in 2017, and 66 in 2018. We also found a few Paiute Sculpin (*Cottus beldingi*) in this stream. A maximum of three trout per day were counted in the SF Rock Creek main channel in 2016, and maximum counts per day in the bottom of SF Tributary 1 were two trout in 2016, one in 2017, and four in 2018. No fish were found in Mossy Pond Creek or SF Tributary 2.

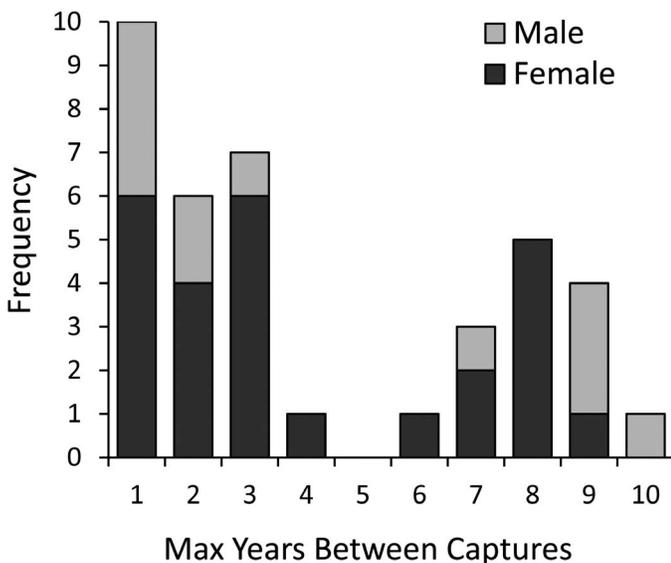


FIG. 2.—Maximum number of years between captures of marked *Rana sierrae* first captured 2009–2013 in three northern Sierra Nevada streams. First captures occurred 2009–2011 in Lone Rock Creek and South Fork (SF) Rock Creek main channel, or 2009–2011 or 2013 in Independence Creek. Last captures occurred 2009–2011 in all three streams; 2013 in Independence Creek, 2015 in Lone Rock Creek and SF Rock Creek main channel, or 2016–2018 in all three streams.

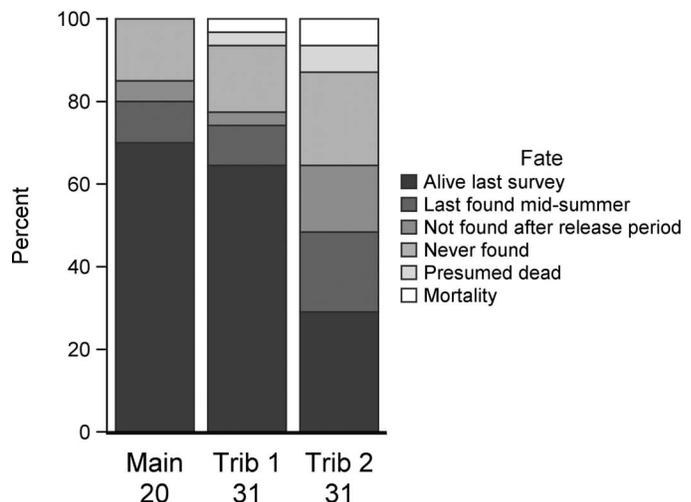


FIG. 3.—Fate of captive-reared frogs released into the South Fork Rock Creek reaches in 2017 and 2018. The number of frogs released into each stream is shown below each bar.

TABLE 4.—Maximum number of subadults and tadpoles counted on a single day for wild *Rana sierrae* in four northern Sierra Nevada streams surveyed 2016–2018. Lone Rock Creek and Independence Creek are perennial streams; the others are intermittent streams.

	Lone Rock Creek	Independence Creek	Mossy Pond Creek	South Fork Rock Creek Main Channel	South Fork Rock Creek Tributary 1	South Fork Rock Creek Tributary 2
Subadults						
2016	4	6	26	1	1	1
2017	4	2	18	0	3	2
2018	23	6	11	3	4	7
Tadpoles						
2016	1	18	9	1	1	107
2017	8	59	4	0	3	18
2018	1	158	4	87	126	525

DISCUSSION

The objectives of this study were to explore the potential of reintroductions as a recovery tool for stream-dwelling *R. sierrae* in their northern range and, if promising, to use demographic data to inform reintroduction designs. In our pilot population augmentation, more than half of the captive-reared frogs survived their first summer, suggesting that further experimentation with reintroductions has merit. In addition, our demographic results provide insights into possible reasons for both the persistence of the small populations in our northern streams and for their low numbers. Our populations had high survival rates of long-lived adults, whereas recruitment and survival of tadpoles and subadults appeared low. Interestingly, populations were larger in intermittent than in perennial streams, possibly because fish are less common where water is not flowing year round. Our results help identify considerations for designing reintroductions as well as areas of further research to increase chances of reintroduction success.

Populations in our study streams were small relative to the hundreds of frogs that can be found in some high elevation lakes (Vredenburg et al. 2010; Brown et al. 2014a; Knapp et al. 2016). The three study reaches surveyed 4 yr earlier continued to have very low abundances of wild frogs (Brown et al. 2019), and these populations likely still remain vulnerable due to their small size (Shaffer 1981). An intermittent stream, Mossy Pond Creek, had the highest abundance, as expected from preliminary surveys. Interestingly, the second highest abundance of wild frogs was found in the intermittent tributaries of SF Rock Creek, which were new to this study. The number of wild frogs in these reaches was similar to those reported by Fellers et al. (2013) in a central Sierra Nevada stream. In that meadow–stream complex, numbers of adults varied annually from 45–115

with no particular trend. Also, the sex ratio in that stream was equal, similar to most of our study streams.

Violations of the population closure assumption of the mark–recapture models would result in overestimates of abundance. Although assumptions like this are ideals that are never fully met, it is important to evaluate the degree to which they are violated. We did document mortality, and it is likely new adults entered our populations during the summer. However, our estimates of low recruitment and high survival suggest that inputs and outputs to the population were relatively small, and our abundance estimates were generally similar to counts. Further, Cormack–Jolly–Seber summer survival estimates were relatively high. These minor violations of the closed population assumption would not change our overall conclusions that populations were small, with larger populations in the intermittent streams.

Rana sierrae generally has been considered a highly aquatic, perennial water species that requires deep lakes for breeding (Bradford 1983; Knapp et al. 2003). Thus, we did not expect to find the larger populations in intermittent streams. How the frogs persist in these intermittent streams is an important question, and studies on habitat use and movements are underway to address this topic. Examining causes of population sizes was beyond the scope of our study, but a likely explanation for the higher frog abundances in the intermittent streams is the lack of fishes which are known to be predators of *R. sierrae* and a primary cause of population declines in mountain lakes (Knapp and Matthews 2000; Vredenburg 2004). A steep barrier protects Mossy Pond Creek frogs from the fishes in the downstream reservoir, and large sections of dry streambed protect the SF Rock Creek frogs from fishes for most of the summer. In contrast, fishes inhabit both perennial streams. Independence Creek is

TABLE 5.—Estimates of 2018 abundance and overwinter survival rates for captive-reared *Rana sierrae* released in 2017 in the South Fork (SF) Rock Creek reaches. Demographic parameter estimates are model averages from Huggins robust design models. Est = estimate; SE = standard error; CI = confidence interval. Number of frogs released in 2017 were 3 female, 8 male in SF Tributary 1 and 6 female, 5 male in SF Tributary 2. Number of frogs released in 2018 was 11 female, 9 male in SF Main Channel; 12 female, 8 male in SF Tributary 1; and 12 female, 8 male in SF Tributary 2.

	South Fork Rock Creek reaches					
	Tributary 1			Tributary 2		
	Est.	SE	CI	Est.	SE	CI
Estimated number of frogs released in 2017 and alive in 2018						
Female	1.0 (of 3)	0.1	1.0–1.9	2.0 (of 6)	0.2	2.0–3.2
Male	5.1 (of 8)	0.4	5.0–7.4	0.0 (of 5)		
Survival rate overwinter from 2017 to 2018						
Female	0.54	0.14	0.27–0.79	0.29	0.13	0.10–0.59
Male	0.56	0.14	0.29–0.80	0.31	0.13	0.11–0.60

downstream from a Lahontan Cutthroat Trout (*Oncorhynchus clarkii henshawi*) conservation area, and we found fishes in the main channel as well as numerous juveniles in the breeding side channels. Lone Rock Creek flows into a large popular recreational fishing reservoir stocked with nonnative trout. We have observed hundreds of adult and juvenile trout and Sacramento Suckers in this reach. Nonnative trout are present in almost all perennial streams within *R. sierrae*'s range, presenting a major conservation challenge for this species. Historical patterns of frog occurrence in intermittent and perennial streams are not known. It is possible that the current populations are isolated remnants of larger populations that once inhabited downstream perennial reaches prior to the introduction of fish. Still, although intermittent streams may not be the most intuitive choice for reintroductions of a highly aquatic species, they may provide important refuges given current conditions and be a realistic alternative to more permanent water, given the widespread presence of nonnative trout (Corlett 2016).

Infection by *Bd* is the other known cause of small *R. sierrae* populations in alpine lakes (Rachowicz et al. 2006; Vredenburg et al. 2010). The low *Bd* loads in the SF Rock Creek reaches in 2018 were similar to those reported for streams in 2009–2011 (Brown et al. 2019). These loads were well below the 600,000 ITS1 copies/swab level associated with morbidity and mortality (Vredenburg et al. 2010; Joseph and Knapp 2018). In addition, we did not find any field mortalities that appeared related to *Bd*. In contrast, the captive-reared frogs appeared to be highly susceptible to the disease based on their reaction to the *Bd* exposure. Future monitoring is needed to determine whether the released captive-reared frogs will become infected with *Bd* or whether the increased population size due to augmentation may change the disease dynamics in the streams (Briggs et al. 2010). The central Sierra Nevada stream population monitored by Fellers et al. (2013) has persisted with low levels of *Bd*, though the effect of the disease on abundances was unknown.

There is no information on historical frog numbers in our study streams to guide expectations for population recovery. It is likely that current numbers reflect the range-wide declines of *R. sierrae* (Vredenburg et al. 2007; Brown et al. 2014a), though it is also possible that these streams may never have supported the large populations once common in lakes. In streams that dry to just a few small pools in the summer, the carrying capacity may be low relative to alpine lakes. Studies on productivity, food supply, and other factors that may affect carrying capacity in these streams would help guide expectations for abundances of recovered populations.

Both survival and recruitment affect population growth rates, persistence, and the potential for recovery (Schmidt et al. 2005; Muths et al. 2011). In species with long lifespans, high survival of adults can sustain populations through periods of low recruitment (Taylor et al. 2006) and population growth is often sensitive to changes in adult survival (Biek et al. 2002; Schmidt et al. 2005; Bertolero et al. 2018). But, without sufficient recruitment, populations can slowly decline (Muths and Scherer 2011). Amphibians like *R. sierrae* that lay many eggs have high reproductive potential and, thus, in the absence of other factors that may depress recruitment, a capacity for fast recovery or population

growth from introduced animals (Pechmann et al. 1991; Alford and Richards 1999; Vredenburg 2004; Knapp et al. 2007). However, there may be a lag between reintroductions and population increases due to long tadpole and/or subadult development (Hunter et al. 2010; Joseph and Knapp 2018).

We found that *R. sierrae* adults can be relatively long-lived, as found in other studies (Matthews and Miaud 2007; Fellers et al. 2013). Although the specific methods for determining ages differed, Matthews and Miaud (2007) and Fellers et al. (2013) estimated maximum ages ranging from 14–16 yr old; the oldest frog in our study was at least 13 yr. Apparent survival of adults was relatively high at two of our study streams, but low at the other two streams. Low apparent survival at Lone Rock Creek may be attributed to the abundance of nonnative trout in the stream. However, frogs at Mossy Pond Creek also had low apparent survival despite the absence of fish. Frogs in this stream may be susceptible to other causes of mortality, but the low apparent survival also may result from emigration to other nearby aquatic habitats. Apparent survival estimates cannot distinguish between mortality and emigration. The demography and movements of frogs in this watershed are currently under study (I. Chellman, personal communication). Apparent overwinter survival rates during this study were similar at Independence Creek, lower at Lone Rock Creek, and higher at SF Rock Creek compared with estimates from 2009–2011 (Brown et al. 2019). Overwinter survival estimates by Fellers et al. (2013) ranged from 0.45–0.95. Thus, apparent overwinter survival can vary among streams and among years.

Recruitment was low in our streams based on estimated recruitment rate, low counts of tadpoles and subadults, and few known breeding areas. However, there was at least some recruitment over a longer time period at the three streams that had been monitored previously. High mortality of eggs, tadpoles, and subadults is common in many amphibians (Alford and Richards 1999). For *R. sierrae*, these younger life stages may be particularly vulnerable because of their prolonged development. The apparent low survival of tadpoles and subadults argues for releasing older individuals.

Low recruitment into the populations may result from a variety of factors. First, few egg masses may be laid due to Allee effects in small populations such as an unbalanced sex ratio, trouble finding mates, or lower reproduction in older individuals (Shaffer 1981). Further, in temperate zones with short growing seasons, females of some amphibians may not breed every year (Muths et al. 2010). In the small populations in our study streams, there were only a few unequal sex ratios in some years, with the bias in opposite directions, though it is possible that the pool of available females may be limited in some years. Our study streams were all ≤ 2.7 km, and frogs are capable of moving relatively long distances with movements documented up to 1.3 km (Brown et al. 2019; Keung et al. in press). Thus, it seems unlikely that frogs would not be able to find mates if present. Population augmentation may help alleviate some of these small population risks. Second, poor placement of egg masses may lead to desiccation or loss from high flows. Each year at least one egg mass was laid in a small pool that dried, stranding the tadpoles. On the other hand, the three breeding locations with tadpoles each year were relatively protected from high spring flows, and the one egg mass we

found was on the underside of a small boulder in a small, protected tributary. Note that we did not search extensively for egg masses in most of our study streams, so further research on this is warranted. Third, predation on tadpoles and subadults by fishes (Knapp and Matthews 2000) likely affects their survival in Lone Rock Creek and Independence Creek. Predation by nonnative Signal Crayfishes (*Pacifastacus leniusculus*; Wiseman et al. 2005) may also occur in Lone Rock Creek. Fourth, newly metamorphosed frogs are particularly susceptible to *Bd* (Rachowicz et al. 2006) although, as discussed, *Bd* loads were low in our streams. Finally, high overwintering mortality of younger life stages may be common in species like *R. sierrae*; little is known about how any of the *R. sierrae* life stages overwinter in streams. Further research on factors affecting survival of eggs, tadpoles, and subadults is needed.

Evaluating reintroductions such as this population augmentation pilot requires some definition of what constitutes success (Seddon 1999). Success can range from the ultimate goal of building a self-sustaining population (Dodd and Siegel 1991) to a series of short-term objectives that provide opportunities for learning (Denton et al. 1997; Hunter et al. 2010; Miller et al. 2014). Our population augmentation in SF Rock Creek served as a pilot test to determine whether reintroductions should even be considered as a restoration tool for the recovery of this endangered species in streams. In the short-term, the release of captive-reared animals was relatively successful. At least half the animals survived to the end of their release summer, and at least 36% of individuals released in 2017 survived to 2018. Further, a companion radio-tracking study found frogs remained near their release pools with no frogs dispersing from the stream (Keung et al. in press).

The lower survival of the captive-reared frogs compared with wild frogs is common in reintroductions (Tavecchia et al. 2009; Bertolero et al. 2018; Cayuela et al. 2019). However, this 'cost of release' may diminish in subsequent generations (Bertolero et al. 2018; Cayuela et al. 2019; Bard-David et al. 2005). Reasons for lower survival are not well known, but suggestions have included dispersal from the stream, higher risk of predation, and stress from a new environment (Armstrong and Seddon 2008). The landscape surrounding our release streams is dry, so it is unlikely frogs would have had incentive to leave the stream channel. Moreover, radio-tracked captive-reared frogs did not leave the streams (Keung et al. in press). We did see a few instances of snake predation in our study, but there did not appear to be a higher rate for captive-reared frogs than for wild frogs. Captive-reared frogs were, on average, smaller than wild adult frogs and thus may have been more susceptible to predation. We cannot evaluate stress, though one frog did die of unknown causes shortly after release. Finally, it is possible that more frogs survived but were cryptic and hard to find; two of the 2017 frogs were not found after their release until 2018.

It is possible that 2017 captive-reared frogs contributed to the increased reproduction in 2018 in the two SF Rock Creek tributaries. For instance, one captive-reared female was found at the breeding pool at SF Tributary 2 in spring of 2018 and a second captive-reared frog was observed depositing eggs in spring of 2019. Also, captive-reared frogs do seem to be reproducing; nine egg masses were found in the SF Rock Creek main channel in 2019, after our study

concluded, which exceeds the numbers of wild frogs known in this reach. Further years of monitoring are needed to clarify the long-term success of the population augmentation.

Reintroductions of at-risk species can be challenging and have had variable success (Dodd and Siegel 1991; Fischer and Lindenmayer 2000; Germano and Bishop 2009). Although our pilot captive-rearing and augmentation seems successful in the short-term, it was not without risk. Our first batch of tadpoles brought into captivity died from a life-support system failure, leading us to collect older, more resilient tadpoles for the second batch. Once the cause of the mortality was identified and resolved, we had 97% success rearing tadpoles to adults. Also, overwinter survival of captive-reared adults was lower than in wild counterparts. On the other hand, there are also inherent risks in doing nothing for critically endangered species (Hunter et al. 1999). Further, there may be opportunities to lessen the risk. For example, we have the opportunity to salvage tadpoles that would otherwise die in a desiccating pool. We are experimenting with releasing some of these tadpoles in other locations in our streams to increase their survival and would use salvaged tadpoles should further augmentation be warranted. Finally, although risks cannot be eliminated and unforeseen events can occur, they also provide opportunity for learning and improving techniques. Monitoring is crucial to maximizing learning from both successes and failures of reintroduction programs, with the ultimate goal of increasing their effectiveness (Armstrong and Seddon 2008; Miller et al. 2014; Muths et al. 2014).

Our demographic data indicated several release design considerations. First, releasing adults seems prudent given their high survival rates and the apparently low survival of the younger life stages. Second, releasing equal numbers of males and females may best reflect ratios in healthy populations. Finally, although there is not sufficient information to set abundance goals for a recovered population, our two largest populations may provide guidelines for what is possible under current conditions. Ultimately, however, stream-specific characteristics may contribute to higher and lower abundances in streams, even under ideal conditions.

Our study also identified information gaps. First, further research is needed on factors that affect recruitment and the survival of eggs, tadpoles, and subadults in streams. Second, information on productivity and other factors affecting the carrying capacities of small intermittent streams could help establish realistic abundance goals for recovered populations in these systems and guide decisions on numbers of frogs to release. Third, studies on interactions between frogs, fish, and crayfish in streams would help develop strategies to promote recovery in streams where these taxa overlap. Finally, longer-term monitoring will assess the ultimate success of our population augmentation as well as provide a longer time series for evaluating demographic parameters. A longer time series could also detect the occurrence, frequency, and implications of population pulses such as those that may have occurred with reproduction in 2018. Studying conditions before and during these pulses may help us understand factors affecting reproductive success.

We set out to evaluate the potential of reintroductions as a recovery tool and to inform the design of a reintroduction program using demographic information and a pilot

population augmentation. In the northern range of *R. sierrae*, we found that populations remained small in three of our study reaches 4 yr after surveys were first conducted, suggesting that conservation actions such as reintroductions may be warranted. However, several challenges remain. The persistence of small populations may be due to the longevity and high survival rates of adults, but low recruitment may prevent these populations from reaching greater abundances or complete recovery. Although apparent survival of captive-reared frogs was lower than with wild frogs, sufficient numbers survived their first summer and winter to merit further experimentation with reintroductions. Decisions about whether to use reintroductions depend on many factors, but our results suggest that this tool may be a promising option for the endangered *R. sierrae* in streams.

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/Herpetologica-D-19-00059.S1>.

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