

Defining relevant conservation targets for the endangered Southern California distinct population segment of the mountain yellow-legged frog (*Rana muscosa*)

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Abstract

The endangered mountain yellow-legged frog (*Rana muscosa*) has been reduced to <10 isolated populations in the wild. Due to frequent catastrophic events (floods, droughts, wildfires), the recent dynamics of these populations have been erratic, making the future of the species highly uncertain. In 2018, a recovery plan was developed to improve the species status by reducing the impacts of various threats (predation, disease, habitat destruction), as well as reinforcing wild populations through the reintroduction of captive-bred frogs. The short-term goal stated in this plan was to reach a minimum of 20 populations of 50 adults each (hereafter, the *20/50 target*), before the species can be considered for downlisting from the U.S. Endangered Species Act. However, there is no guarantee that this *20/50 target* will be sufficient to ensure the species persistence in the long run. Using 19 years of mark-recapture data, we estimated populations' demographic trends and assessed the viability of *R. muscosa* from a starting state of 20 populations of 50 adults each (i.e., the downlisting criteria). Our results reveal that, from this *20/50 state*, the species has high chances of persistence only at a short time horizon (50 years). Moreover, >80% of populations would be extinct 50 years later. Therefore, the species will not be able to persist without implementation of the reintroduction program. We found that it is more important to increase the number of suitable sites occupied by *R. muscosa* than to simply reinforce or augment existing populations. Expanding the current distribution by establishing new populations at suitable sites, even after the “20 populations” mark has been reached, would increase the likelihood of the species' persistence in the longer term.

KEYWORDS

amphibian decline, California, conservation target, data-driven conservation, endangered species act, environmental stochasticity, population viability analysis, species recovery plan

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1 | INTRODUCTION

The mountain yellow-legged frog (*Rana muscosa*; Figure 1) is a highly threatened anuran endemic to California. Once widely distributed in high-altitude streams and lakes across mountain ranges of southern California and the southern Sierra Nevada, *R. muscosa* populations have been declining since the late 1960's (Bradford et al., 1994; Jennings & Hayes, 1994; Stebbins & Cohen, 1997; Knapp & Matthews, 2000). The southern California distinct population segment (DPS) of the mountain yellow-legged frog has since been extirpated from all its range except at a few sites in three mountain ranges (Figure 2): the San Gabriel, San Bernardino and San Jacinto mountains (Backlin et al., 2015; Schoville et al., 2011; Stebbins, 2003). A population of *R. muscosa* occurred in the Palomar mountains (Figure 2), but all recent survey efforts failed to detect any sign of the species (Backlin et al., 2015). Between 2000 and 2009, surveys were conducted at 150 streams with suitable habitat throughout the historical range of the species, but only nine small fragmented populations were found. These populations proved to be geographically and genetically isolated (Backlin et al., 2015). Populations of mountain yellow-legged frogs that occur further north, in the Sierra Nevada, were considered as part of the *R. muscosa* species complex (Macey et al., 2001), but they are now recognized as a fully distinct species, *Rana sierrae* (Vredenburg et al., 2007) with only parts of the southern Sierra Nevada being occupied by *R. muscosa* (northern California DPS of the mountain yellow-legged frog). Populations of *R. sierrae* and *R. muscosa* from the Sierra Nevada Mountains are not covered in this study.

Overall, the underlying causes of the decline of southern populations of *R. muscosa* remain poorly understood (Backlin et al., 2015; Schoville et al., 2011). Predominant



FIGURE 1 Photo of the species. Mountain Yellow Legged Frog (*Rana muscosa*). Credit: Adam Backlin

factors include predation by nonnative fish (introduced trout) as well as catastrophic environmental disturbances such as floods, droughts, and wildfires (Backlin et al., 2015; USFWS, 2018a). Chytridiomycosis is another potentially important threat (Russell et al., 2019). Indeed, all known populations of *R. muscosa* were found positive (prevalence 6%) for the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (Backlin et al., 2015), and a mass die-off, presumably due to this fungus, occurred at one site (Devils Canyon) in the Fall/Winter 2013–2014. Other possible threats to their native habitat include illegal cannabis cultivation and suction dredge mining, as well as legal recreational activities, fire suppression and roadwork construction (USFWS, 2018a).

Southern populations of *R. muscosa* are currently listed as Endangered by the IUCN (IUCN, 2013), the U.S. Fish and Wildlife Service (southern California distinct population segment of the mountain yellow-legged frog was listed as endangered in 2002 under the Endangered Species Act,

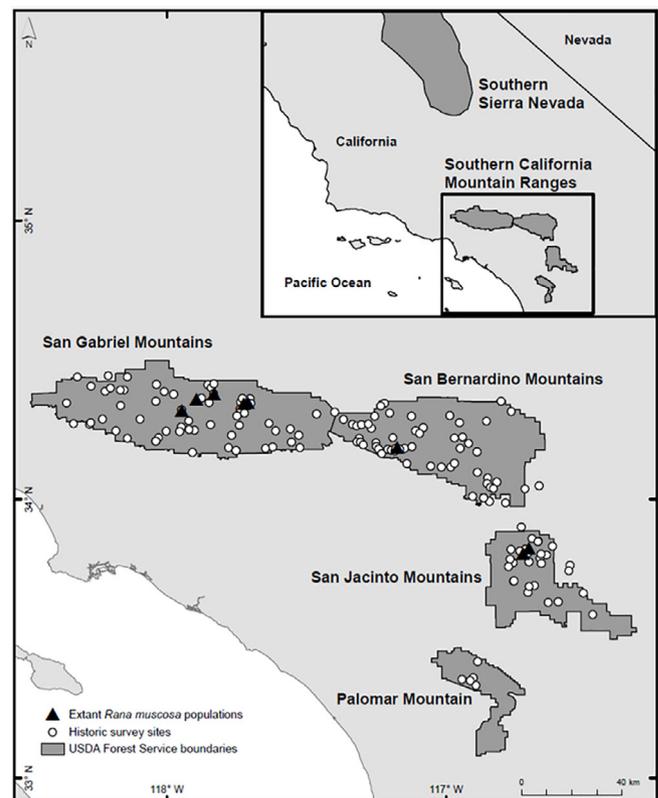


FIGURE 2 Map of study site. Location of survey sites (open circles) and extant populations (black triangles) of Mountain Yellow-Legged Frog *Rana muscosa* in southern California. The extant populations are located at (1) Bear Gulch, (2) Little Rock Creek, (3) Vincent Gulch, (4) Big Rock Creek, (5) Devils Canyon, (6) City Creek, (7) Fuller Mill Creek, and (8) Dark Canyon. All historical populations from the Palomar Mountain are now extinct (Backlin et al., 2015). The inset shows the location of the main map in California

as amended; 16 U.S.C. 1531 *et seq.*; USFWS, 2002), as well as the State of California (California Endangered Species Act, Title 14, California Code of Regulations, Section 670.5). In 2018, a recovery plan was completed by the U.S. Fish and Wildlife Service with the goal of rapidly improving the species conservation status (USFWS, 2018b). The recovery plan relies on a set of actions to improve knowledge of the species' ecology and the main drivers of its decline, as well as reduce the impacts of various factors that have been identified as threats or obstacles to the species recovery (USFWS, 2018b). The Recovery Implementation Strategy includes specific actions (e.g., nonnative predator removal, fuel reductions to reduce wildfire risk) targeted toward predation and disease, as well as habitat destruction, modification, and curtailment (USFWS, 2018c). In addition to these threat mitigation actions, the recovery plan relies on the reintroduction of captive-bred frogs into the wild to augment existing populations and reestablish new populations at suitable sites (USFWS, 2018b, 2018c).

Before the species can be considered for reclassification, one criterion, as stated in the recovery plan (USFWS, 2018b), is to reach at least 20 populations with a minimum of 50 adults each. When it was set, this numeric objective (hereafter the *20/50 target*) was considered a good conservation target to ensure the persistence of *R. muscosa* in its southern California range, but its relevance has not yet been fully evaluated. The goal of this study was to quantitatively assess the relevance of this target by predicting the likelihood of the species persistence at a 50-year horizon, if the *20/50 target* was met. To put this criterion into perspective and further inform the recovery plan's objectives and strategy, we also assessed the species viability for a broader range of numeric targets, which could serve as alternative objectives under different risk acceptance scenarios (Sanderson, 2006; Schwartz et al., 2018). For this purpose, we first performed a demographic analysis using 19 years of mark-recapture data collected on the extant populations of *R. muscosa*, followed by a population viability analysis to simulate species trajectories under a defined set of alternative scenarios. The analyses of the mark-recapture data provided estimates of demographic parameters, environmental stochasticity, and density-dependent patterns. These parameters were used in a stochastic projection model to forecast population trajectories across time and assess the risk of extinction of *R. muscosa* populations at a 50-year time horizon.

2 | MATERIAL AND METHODS

2.1 | Mark-recapture data collection

We used mark-recapture data collected annually from 2001 to 2019 at eight different sites (see Figure 2): (1) Bear

Gulch, (2) Little Rock Creek, (3) Vincent Gulch, (4) Big Rock Creek and (5) Devils Canyon, located in the San Gabriel Mountains; and (6) City Creek, located in the San Bernardino Mountains (7) Fuller Mill Creek and (8) Dark Canyon, located in the San Jacinto Mountains. We note that a typical *R. muscosa* site in our sample represents an intermittent stream section of ca. 2.75 km in length. A ninth location, Tahquitz Creek located in the San Jacinto Mountains was excluded from the dataset because it was only rediscovered in 2009 and has been known to be occupied by only five adult female frogs. The historical population that once existed on Palomar Mountain appears to be extirpated. Adult frogs were marked with passive integrated transponder tags. The analyses presented here pertain only to adult individuals; we only tagged individuals larger than 50 mm, snout to vent length (Backlin et al., 2015).

Each population's monitoring followed a robust design, where each year corresponds to a primary occasion. The number of secondary sampling occasions was variable among sites and years, but two consecutive surveys were typically separated by 1–3 weeks. The annual monitoring effort at each site varied from 1 to 10 mark-recapture surveys (secondary occasions), for an average of 2.9 (SD = 1.4) surveys per site per year. These secondary occasions (i.e., repeated surveys within the same season) provided the data required to account for imperfect detection (Williams et al., 2002). Across the 19 years of study, 924 adult frogs were marked across the eight study sites, and the total number of resightings was 2119 detections.

2.2 | Parameter estimation

In the first step of the analysis, we estimated annual population sizes at each site, using a within-year closed population mark-recapture model (Williams et al., 2002). Because only adult frogs are marked, here the term “population” refers to the population of adult frogs present at a site, each year between 2001 and 2019. We used a hierarchical mark-recapture modeling approach based on data-augmentation (Royle & Dorazio, 2008; see Appendix A1 for details). The closed population model was applied to each site and each year separately, but inside the same hierarchical Bayesian analysis, thus allowing shared parameters (e.g., detection probability) and the estimation of inter-annual population growth rates as derived parameters. Our model explicitly estimated probability of detection, thus accounting for imperfect detection of marked frogs. Because of data limitation, detection probability was modeled as a constant parameter across years, sampling occasions and sites. All sites and years were

analyzed together to maximize the amount of data used to inform the detection parameter, but the model allowed each site to have a distinct population trajectory.

Next, we plugged estimates of population growth rates from the previous step in a log-normal model to quantify the amount of spatial (i.e., across-site) and temporal (i.e., environmental) variability. Spatial variability captures differences in quality (e.g., availability of food or shelters) among sites, while temporal variability captures the effects of stochastic environmental fluctuations over time (e.g., variations in food availability, or the occurrence of disturbing events such as wildfires). This analysis provided us with estimates of the standard deviation (on the log scale), across year and across sites, in population growth rates. Full details on the model used for this analysis are provided in Appendix A2.

Finally, we estimated the carrying capacity of a typical *R. muscosa* site (i.e., a section of stream of ca. 2.75 km in length), which was used as the maximum population size that could be reached at any site in the simulations. For this analysis we used data from Little Rock Creek, because this was the only site where the population had shown enough growth to get close to carrying capacity. This population displayed an exponential growth during several years, followed by a deceleration and stabilizing phase at ~600 frogs (Figure 3). This pattern suggests that the Little Rock Creek population approached carrying capacity at that time. To estimate the carrying capacity parameter K , we used Ricker's parameterization of density-dependence (Ricker, 1954) in a discrete-time logistic growth model (Eberhardt et al., 2008), as explained in Appendix A3.

All these analyses were done in a Bayesian framework using Markov Chain Monte Carlo algorithms (MCMC) implemented in program JAGS through the rjags package (Plummer, 2013) in R (R Core Team, 2020). For each analysis, we ran three chains initialized with a different set of initial values. We used a burn-in period of 5000 MCMC iterations followed by 100,000 MCMC iterations to sample the posterior distribution. For parameter inference, we thinned the posterior samples at a ratio 1/10 samples, for a total of 30,000 samples across the three chains. Chain convergence was assessed visually with sample path plots and using the Brooks–Gelman–Rubin diagnostic “BGR” (Brooks & Gelman, 1998). Values of R close to 1.00 indicate good convergence of the MCMC.

2.3 | Population projections

We used a simulation approach to project demographic trajectories of *R. muscosa* under different scenarios and assess the chances of persistence of the species over

50 years, which is a fairly short time horizon. Given the poor current state of the species, there is a sense of urgency and short-term issues will likely be addressed by managers before longer-term persistence. The scenarios we investigated represent different possible statuses for *R. muscosa* populations of southern California. These various scenarios could be viewed as alternative delisting targets and were used as the initial population state for the demographic projections. Following the logic of the 20/50 target, these scenarios were built by varying two key parameters: (i) the number of sites (S) holding *R. muscosa* populations (e.g., reintroduction sites), which varied between 5 and 50 sites; and (ii) the starting population size (N_0) of adult frogs at each site (e.g., number of frogs initially reintroduced), which ranged from 5 to 100 individuals.

Our model of population projection included demographic and environmental stochasticity and parameter uncertainty, as well as a carrying capacity (i.e., population size limit). This model was parameterized using estimates, obtained from the previous step (mark-recapture analysis), of the following variables: (i) the average value of population growth rate; (ii) spatial (site) and temporal (year) variance in population growth rates; and (iii) site carrying capacity (K). Population trajectories were simulated using the procedure described in Appendix A4. Population growth at each time step varied among sites and across years according to the spatial and temporal variance quantified from the data analyses (see above).

Using 1000 simulations for each scenario, we quantified the risk of extinction of the species as a whole, and of populations, using the following metrics: (i) risk of species extinction (i.e., the probabilities of full- and quasi-extinction of the species after 50 years, using $N = 10$ as the threshold for quasi-extinction); (ii) the probability that less than two populations will be above the quasi-extinction threshold after 50 years; (iii) the proportion of populations that went fully extinct after 50 years; and (iv) population persistence; (i.e., the expected number of populations left after 50 years). We define a quasi-extinct population as one retaining a few (<10) individuals and a fully extinct population as one with no remaining individuals.

3 | RESULTS

3.1 | Demographic parameters

In the three analyses, the MCMC sampling procedure showed good mixing and all chains had converged by the end of the burn-in period (BGR <1.02 in all three analyses). Detection probability was estimated at 0.10 (SE = 0.006, 95% CI = [0.09, 0.12]) per survey. The population

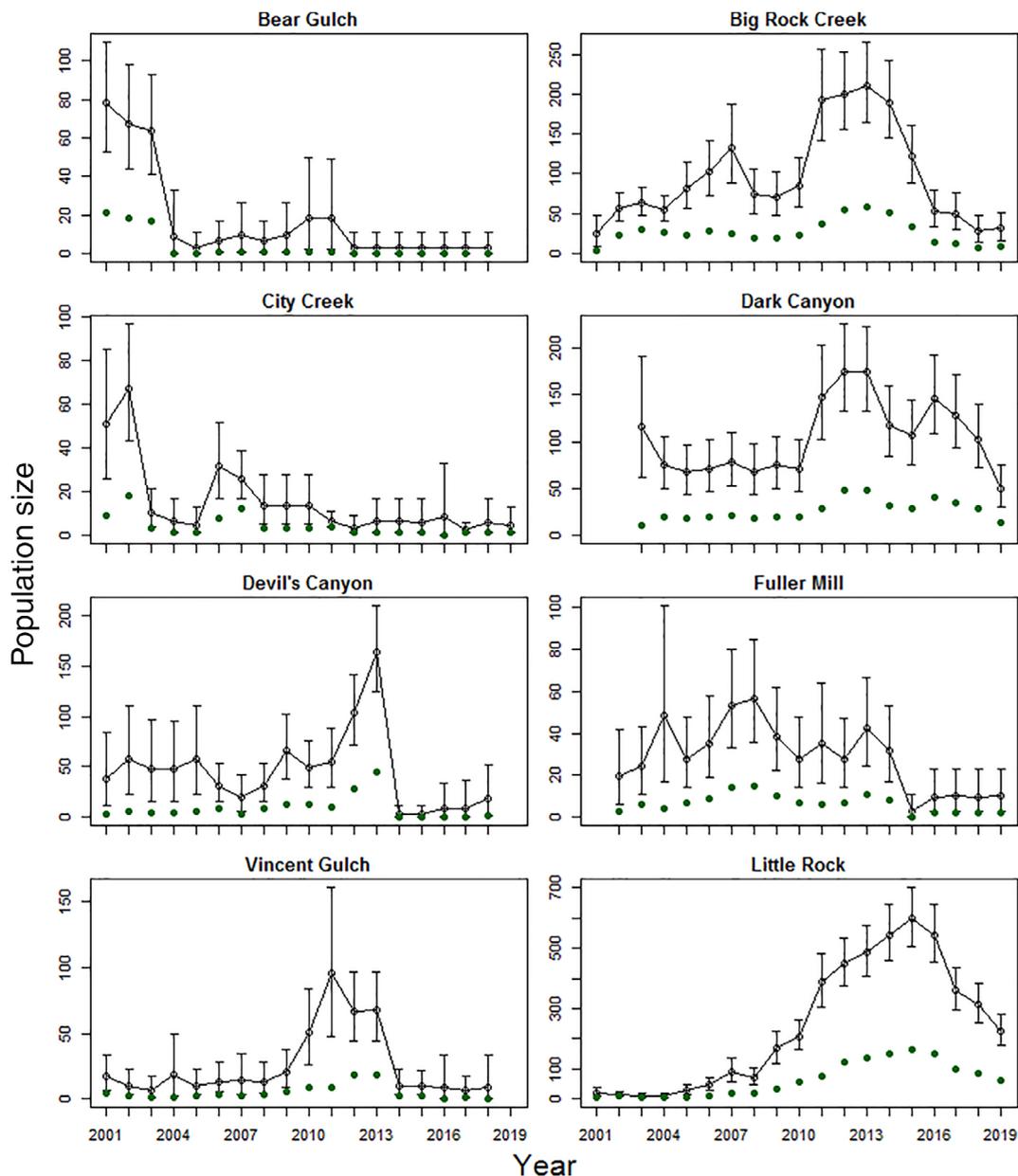


FIGURE 3 Past population trajectories. Estimated population size at each site over the last 19 years. Note that the y-axis scale is not the same on all graphs. The open circles and black lines correspond to the population size values estimated from the population analysis, thus corrected for imperfect detection. The dark green dots are raw counts from the data: number of frogs encountered during annual surveys. These latter values are not corrected for detection, and thus underestimated. They are only provided here for reference

dynamics of each site, between 2001 and 2019, are shown in Figure 3. The highest observed local abundance was reached in 2015 at Little Rock Creek, where population size was estimated as $N = 597$ frogs (SE = 50.5; 95% CI = [503, 701]). This population, which had been static at very low numbers until 2005, experienced a rapid growth until 2015, and had since been declining. By 2019, local abundance at Little Rock Creek dropped to $N = 225$ frogs (SE = 27, 95% CI = [177, 282]), less than half of what it was in 2015, but still considerably higher than before 2009. This illustrates the high level of unpredictability in

R. muscosa population dynamics. Big Rock Creek, Dark Canyon and Devils Canyon also had large populations at some point during the 20-year study (respectively: $N = 211$, $N = 175$, and $N = 164$) and declined after these peaks to lows of <50 frogs by the end of the survey period. In recent years, all sites' populations have in fact been declining (Figure 3).

The average population growth rate, across all sites and years, was 0.796 (SE = 0.170, 95% CI = [0.462, 1.130]). This means that *R. muscosa* populations are declining by an average of 20% each year. Despite periodic

increases in population size, all populations have been declining on average over the 19 years of study, except at Little Rock Creek (Table 1). But the most striking features in these populations' dynamic are the spatial and temporal

variabilities. The across-site standard deviation of population growth rates amounts to 46% (SE = 21%) of their average value, and the across-year standard deviation amounts to 99% (SE = 6%).

Finally, from the Little Rock Creek dataset, we estimated the carrying capacity of a suitable site at $K = 590$ individuals (SE = 15.4, 95% CI = [559, 620]). To remain conservative, we decided to use $K = 500$ in the simulations. Indeed, we cannot be sure that every suitable site would necessarily be able to hold quite as many frogs as Little Rock Creek.

TABLE 1 Estimates of population growth rates: Average population growth rate at each site across 19 years

Site	Growth rate	SE	LCI	UCI
Bear Gulch	0.387	0.110	0.172	0.602
Big Rock Creek	0.967	0.207	0.561	1.373
City Creek	0.833	0.173	0.493	1.173
Dark Canyon	0.918	0.203	0.520	1.317
Devils Canyon	0.745	0.158	0.435	1.055
Fuller Mill Creek	0.865	0.185	0.503	1.228
Vincent Gulch	0.855	0.183	0.497	1.212
Little Rock Creek	1.056	0.232	0.601	1.510

Note: The estimated growth rate is provided, along with the standard error (SE) and the lower (LCI) and upper (UCI) limits of the 95% CI.

3.2 | Population projections

Results from population projections revealed that, for species persistence after 50 years, the number of populations has more influence than the number of individuals per population (Table 2). From a purely demographic perspective, our modeling indicates that to avoid the risk of full extinction of the species at a 50-year time

N_0	Initial number of populations									
	5	10	15	20	25	30	35	40	45	50
100	34%	11%	3.0%	0.8%	0.4%	0.0%	0.1%	0.0%	0.0%	0.0%
95	32%	12%	4.5%	1.4%	0.4%	0.1%	0.0%	0.0%	0.0%	0.0%
90	33%	12%	4.4%	1.4%	0.2%	0.1%	0.0%	0.0%	0.0%	0.0%
85	34%	12%	3.9%	1.7%	1.1%	0.0%	0.0%	0.0%	0.0%	0.0%
80	35%	12%	3.5%	1.4%	0.5%	0.3%	0.1%	0.0%	0.0%	0.0%
75	33%	11%	4.3%	1.1%	0.9%	0.1%	0.1%	0.0%	0.0%	0.0%
70	35%	11%	3.6%	1.2%	0.6%	0.0%	0.0%	0.0%	0.0%	0.0%
65	34%	11%	4.6%	1.9%	0.7%	0.0%	0.2%	0.0%	0.0%	0.0%
60	34%	14%	4.1%	1.6%	0.8%	0.2%	0.1%	0.0%	0.0%	0.0%
55	35%	11%	3.5%	0.6%	0.5%	0.2%	0.0%	0.0%	0.0%	0.0%
50	33%	13%	5.9%	1.0%	0.6%	0.0%	0.1%	0.0%	0.0%	0.0%
45	36%	16%	4.6%	1.5%	0.5%	0.3%	0.1%	0.0%	0.0%	0.0%
40	38%	13%	4.9%	2.2%	1.0%	0.3%	0.0%	0.1%	0.0%	0.0%
35	37%	13%	6.6%	1.6%	0.5%	0.2%	0.1%	0.0%	0.0%	0.0%
30	37%	15%	6.5%	1.7%	1.1%	0.2%	0.1%	0.2%	0.0%	0.0%
25	40%	14%	6.4%	1.8%	1.2%	0.5%	0.4%	0.0%	0.0%	0.1%
20	43%	16%	5.7%	3.2%	0.6%	0.3%	0.2%	0.0%	0.0%	0.0%
15	42%	18%	6.0%	2.4%	0.8%	0.3%	0.1%	0.0%	0.0%	0.0%
10	46%	23%	10%	4.3%	1.9%	0.6%	0.3%	0.2%	0.0%	0.1%
5	51%	29%	12%	7.0%	3.7%	1.7%	1.1%	0.4%	0.3%	0.1%

Note: Here, species extinction is defined as all populations going fully extinct (i.e., $N = 0$ frogs). Each scenario is defined by (i) the initial number of extant populations (columns) and (ii) the initial population size (N_0) of each population (row). The color gradient represents an arbitrary scale for the risk of extinction (red = high; green = low).

TABLE 2 Probability of full extinction: Probability of species extinction, after 50 years, under various scenarios

TABLE 3 Proportion of populations extinct: Proportion of populations expected to be extinct after 50 years

N_0	Initial number of populations									
	5	10	15	20	25	30	35	40	45	50
100	80%	80%	80%	80%	80%	81%	80%	80%	80%	80%
95	80%	81%	80%	80%	80%	80%	80%	80%	80%	80%
90	81%	80%	80%	80%	81%	80%	80%	80%	81%	80%
85	81%	80%	81%	80%	80%	80%	81%	80%	80%	80%
80	81%	81%	80%	80%	80%	81%	80%	81%	81%	81%
75	81%	81%	81%	81%	80%	81%	81%	80%	81%	81%
70	81%	81%	80%	81%	81%	81%	81%	81%	81%	81%
65	81%	81%	81%	81%	81%	81%	81%	81%	81%	81%
60	80%	81%	82%	81%	81%	81%	81%	81%	81%	81%
55	81%	81%	81%	81%	81%	81%	81%	81%	81%	81%
50	80%	81%	82%	81%	81%	81%	81%	81%	81%	81%
45	81%	81%	82%	81%	81%	81%	81%	82%	82%	81%
40	83%	82%	82%	82%	82%	81%	82%	82%	82%	82%
35	83%	82%	82%	82%	82%	82%	82%	82%	82%	82%
30	82%	82%	83%	82%	82%	82%	82%	82%	82%	82%
25	83%	83%	83%	83%	83%	83%	83%	83%	83%	83%
20	84%	83%	83%	83%	83%	83%	83%	83%	83%	83%
15	84%	84%	84%	84%	84%	84%	84%	84%	84%	84%
10	85%	86%	85%	86%	85%	85%	85%	86%	85%	86%
5	88%	88%	87%	88%	88%	88%	88%	88%	88%	87%

Note: Each scenario is defined by (i) the initial number of extant populations (columns) and (ii) the initial population size (N_0) of each population (row).

horizon, at least 30 populations are required (Table 2). This result is almost completely independent of the initial population size, as long as $N_0 > 10$. Results were almost identical when using the quasi-extinction threshold ($N < 10$) as a criterion (see Appendix A5).

Under the scenario corresponding to the delisting criteria of $S = 20$ and $N = 50$, as stated in the species recovery plan, the risk of species extinction 50 years later would only be 1% (Table 2). Using quasi-extinction, this risk would be of 1.7%, still pretty low (Appendix A5). Nevertheless, if we take a closer glance at the condition after 50 years of the whole species segment targeted here, the predictions look much gloomier. About 16 out of these 20 populations (81%; see Table 3) would be expected to have gone extinct by the 50-year mark. On average, we thus would expect only 3 or 4 populations (mean = 3.5, SE = 1.7) to remain.

Across all the scenarios assessed, it is expected that between 80% and 88% of all *R. muscosa* populations will go extinct every 50 years (Table 3, Appendix A5). We highlight the fact that these predictions are independent of the initial number of populations, as we would expect,

but also are only very marginally improved by the initial number of individuals. This latter point is due to the high level of stochasticity. Even a fairly large initial population might quickly crash, due to unpredictable disturbances, as we have seen happen in some of the extant populations in the last 19 years (Figure 3).

4 | DISCUSSION

The analysis of the 19 years of mark-recapture data revealed that the demography *R. muscosa* is characterized by a high level of unpredictability, most populations showing periodic bouts of large growth and decline. Such levels of fluctuations are not uncommon in amphibians (Muths et al., 2017) and do not necessarily represent a threat to their viability (Pechmann et al., 1991; Meyer et al., 1998). However, given the small number of locations of *R. muscosa* and the fact that since 2015 all major populations have been declining (Figure 3), this situation could become highly problematic if the species does not have enough resiliency to quickly grow back after major

bouts of declines. The onset of the recent declines observed in most populations is likely attributed, at least in part, to a severe drought, that started in 2012 (Griffin & Anchukaitis, 2014), and has contributed to the continued decline of water levels at these sites. But overall, the mechanisms responsible for the various populations' ups and downs observed in the past remain largely unknown, and more importantly they are unpredictable events (like droughts, fires, *Bd* die-offs, etc.). To include this property in our demographic projections, we used stochastic simulations as is classically done in population viability analyses (Beissinger & McCullough, 2002). Here, it is important to understand that environmental stochasticity is used as a robust and convenient way to represent the occurrence of unpredictable disturbances in the future. This is necessary to avoid overoptimistic results from the simulations. Nonetheless, it does not mean that past periodic population growth and decline are only due to chance. They were most likely driven by real ecological disturbance, such as fires and droughts. More details about the disturbances that have occurred in the past at each site are provided in Supporting Information (Appendix A6).

In our projection model, population growth rates varied at each time step due to temporal stochasticity but were assumed to be temporally independent. Two potential limits could exist with this simplified approach. First, temporal autocorrelation might exist, as suggested by some of the populations' past trajectories (Figure 3) that show irregular cycles of growth and decline. *R. muscosa* is a long-lived species with high recruitment potential that can stay in the tadpole stage for multiple years. Therefore, apparent cycles of growth and decline could be due to a lagged response to environmental fluctuations (e.g., fluctuations in food and breeding habitat availability). Alternatively, these apparent cycles could be random and not necessarily imply any real underlying pattern. We tested the data for temporal autocorrelation and we found that it was very weak and not statistically significant ($r = .065$, $p = .438$).

Second, we could also have expected a negative relationship between annual growth rate and population size (i.e., compensatory density dependence), due to increased intraspecific competition among frogs at higher density. In fact, we found some evidence for that relationship, but it was weak ($\beta = -0.003$, $SE = 0.001$) and explained only about 5% of the observed variance in growth rates ($R^2 = 0.056$). So, it did not seem to be a crucial component for our population projection model. Nonetheless, to assess if this level of density dependence could influence our projections results, we reran our analyses, including this relationship in our simulation model. Results were very close to those presented here (<10% differences in all our simulated metrics) and slightly more optimistic for the

future of *R. muscosa*, due to the compensatory effect of density dependence on declining populations. Since these latter results would not have changed our broad conclusions, we chose to remain more conservative and show only the results from the analysis without compensatory density dependence.

Another potential limit of our study is due to the low detectability of frogs on the field. Detection probability *per-secondary-occasion* was estimated at 0.10 [0.09, 0.12], which led to a seasonal detection probability (p^*) of .25, on average. Low detectability adds uncertainty in our population estimates, as reflected by some of the large confidence bars on Figure 3. Nonetheless, this uncertainty was explicitly quantified by our hierarchical mark-recapture model and fully propagated throughout the rest of the analyses.

In all scenarios investigated, we found that between 80% and 88% of populations are expected to go extinct after 50 years. This prediction is driven by the fact that *R. muscosa* population dynamics are characterized by (i) an overall strong negative demographic trend corresponding to an annual decline averaging 20% across all populations, and (ii) a high level of unpredictability (modeled as environmental stochasticity), which is responsible for erratic population trajectories (Figure 3). This result predicts a somber future for *R. muscosa* as a species and illustrates the importance of using ongoing conservation activities to continue to learn about factors affecting species viability. To improve the status of the species, managers could consider reversing the decline and avoiding catastrophic events by acting upon the threats presumed to be the most detrimental, such as those targeted by the recovery plan (predation by non-native fish, wildfires, disease). Second, our results illustrate the importance of building resiliency of the species in this part of its range by establishing enough subpopulations at suitable sites. This would help the species to better withstand unpredictable catastrophic events. This latter approach relies heavily on the reintroduction of captive-bred frogs or harvest and head-starting of wild frogs as a source.

Reintroduction of captive-bred individuals has also been identified as a key conservation tool for the recovery of *R. sierrae* (MYLF ITT, 2018). For that closely-related species, a recent study (Brown et al., 2020) suggested that the chances of success can be increased by releasing adults in the wild, which have much higher chance of survival, rather than juveniles. Our results provide further insights that can help inform a sound reintroduction strategy. We found that it is more important to increase the number of suitable sites occupied by *R. muscosa* than to simply reinforce or augment existing populations. Indeed, demographic resiliency will only occur if enough

sites are holding *R. muscosa* populations at any point in time. Therefore, from a purely demographic perspective, an effective strategy would be to supplement the southern California *R. muscosa* population segment by releasing frogs at favorable sites that are currently unoccupied by the species. This conclusion, however, must be interpreted with caution. Indeed, the success of such a reintroduction strategy would strongly depend on the ability to accurately characterize and find patches of favorable habitat (Malone et al., 2018). A major risk would be to release frogs in suboptimal habitat. The study of Brown et al. (2020) on *R. sierrae* suggests that intermittent streams are more suitable than perennial streams because they are less likely to host nonnative predatory trout. This provides useful guidance for the choice of new release sites. In addition, careful assessment of the reintroduction strategy (e.g., using pilot trials and simulations) with respect to how many frogs to release at each new location and how frequently would maximize success. Disease mitigation strategies are also likely to influence successful population establishment. Currently limited tools are available to effectively manage this and hopefully development of new robust strategies will greatly increase population persistence and establishment success.

Finally, it is important to point out that our viability analyses did not take population genetics' considerations into account, a component that plays a crucial role in species persistence over the long run (Franklin & Frankham, 1998; Sanderson, 2006). But *R. muscosa* is in such a state of urgency that the current priority is to ensure demographic viability in the short term. But, as the species recovers, it will be important to devise a reintroduction plan that not only relies on demographic predictions, but also integrates habitat suitability and population genomics (Malone et al., 2018).

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CONFLICT OF INTEREST

The authors report no conflict of interest.

AUTHOR CONTRIBUTIONS

Thierry Chambert and Robert N. Fisher conceived the ideas. Thierry Chambert designed and completed the analyses. Robert N. Fisher, Adam R. Backlin, Elizabeth Gallegos and Bradd Baskerville-Bridges designed the field study and collected the data. Thierry Chambert led the writing. All authors contributed to the writing of the final manuscript.

ETHICS STATEMENT

This research followed ethical standards. Field surveys and animal marking was done under U.S. Federal Permit TE-045994 and CDFW Entity Permit #838.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.44j0zpcgb>

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SUPPORTING INFORMATION

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