Untangling multi-scale habitat relationships of an endangered frog in streams to inform reintroduction programs

CATHY BROWN,† A. JUSTIN NOWAKOWSKI, NEIL C. KEUNG, SHARON P. LAWLER, AND BRIAN D. TODD

1Stanislaus National Forest, USDA Forest Service, 19777 Greenley Road, Sonora, California 95370 USA
2Working Land and Seascapes, Conservation Commons, Smithsonian Institution, Washington, D.C. 20013 USA
3Moore Center for Science, Conservation International, Arlington, Virginia 22202 USA
4Center for Watershed Sciences, University of California, 425 La Rue Road, Davis, California 95616 USA
5Department of Entomology and Nematology, University of California, 1 Shields Avenue, Davis, California 95616 USA
6Department of Wildlife, Fish, and Conservation Biology, University of California, 1 Shields Avenue, Davis, California 95616 USA

Citation: Brown, C., A. J. Nowakowski, N. C. Keung, S. P. Lawler, and B. D. Todd. 2021. Untangling multi-scale habitat relationships of an endangered frog in streams to inform reintroduction programs. Ecosphere 12(10):e03799. 10.1002/ecs2.3799

Abstract. Successful reintroductions of endangered species rely on comprehensive knowledge of habitat requirements across spatial and temporal scales. To inform designs of reintroduction programs, we studied habitat selection of the federally endangered Sierra Nevada yellow-legged frog (Rana sierrae) in streams in its northern range. We quantified multi-scale habitat use across diverse streams, habitat types within streams, and seasonal flows. In one intermittent stream, we compared habitat selection between wild and captive-reared frogs that were released as a population augmentation. We analyzed habitat selection of seasonal habitat unit types (e.g., pool, riffle, cascades) and dimensions, and microhabitat hydrology and cover. R. sierrae appeared able to meet its ecological requirements in a variety of habitats. Study streams ranged from third-order perennial streams to first-order intermittent headwater creeks. Perennial streams retained a variety of habitats across flows whereas intermittent streams dried to just a few pools. Frogs used all seasonal habitat types but selected deeper pools most often relative to available habitats in intermittent streams and selected riffles or showed no preference in perennial streams. Frogs avoided fast deep-water microhabitats, but, otherwise, preferred flowing water or deeper water without flow. Our results suggest that diverse streams can be considered candidates for reintroductions. Within intermittent streams, deeper perennial pools may provide more stable release sites, whereas non-pool habitats may be safer in perennial streams with fish. Importantly, captive-reared frogs selected similar habitats as wild frogs, suggesting that captivity does not alter habitat selection behaviors post-release and that reintroduction designs for this species can be based on wild frog preferences. By improving our understanding of how habitat use varies among different types of streams and differs seasonally in response to changing habitat conditions, our results inform the design of effective reintroduction programs for frogs in streams.

Key words: amphibian; captive-reared; habitat selection; hydrology; population augmentation; Rana sierrae; Sierra Nevada yellow-legged frog; spatial–temporal variation; stream habitat.

Received 10 April 2021; accepted 6 May 2021. Corresponding Editor: Michael T. Bogan.
Copyright: © 2021 The Authors. Ecosphere published by Wiley Periodicals LLC on behalf of Ecological Society of America. This article has been contributed to by US Government employees and their work is in the public domain in the USA. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† E-mail: cathy.brown@usda.gov
INTRODUCTION

Successful reintroductions of endangered species depend on a thorough knowledge of their habitat use to ensure reintroduction sites meet critical biological needs (Dodd and Seigel 1991, Armstrong and Seddon 2008, Stadtmann and Seddon 2020). Reintroducing species to low-quality habitats or habitats where causes of declines still remain can lead to failed reintroductions (Fellers et al. 2007, Bennett et al. 2013, Berger-Tal et al. 2020). Understanding habitat needs can identify habitat-related causes of declines (Jachowski et al. 2011, Bennett et al. 2013), elements necessary for population persistence (Cheyne 2006, Zhang et al. 2017), and effective reintroduction strategies (Rantanen et al. 2010, Bodinof et al. 2012).

Failure of reintroduced animals to recognize suitable habitat is a common reason for unsuccessful reintroductions (Stamps and Swaisgood 2007, Berger-Tal et al. 2020). Released animals often leave seemingly high-quality habitats leading to higher mortality risks both when traveling (Tuberville et al. 2005, Germano and Bishop 2009) and if they ultimately settle in poorer quality habitats (Stamps and Swaisgood 2007, Rantanen et al. 2010, Berger-Tal et al. 2020). This may be particularly problematic for captive-reared animals whose rearing environments differ from those in the wild (Jule et al. 2008, Tetzlaff et al. 2019). Understanding whether habitat selection behaviors are innate or learned from cues based on early experiences can inform reintroduction designs, including whether conditioning tactics like soft releases, environmental enrichments, or behavioral trainings are warranted (Tuberville et al. 2005, Stamps and Swaisgood 2007, Tetzlaff et al. 2018). It has been suggested that captive-reared amphibians and reptiles tend to retain ecologically appropriate behaviors (Bloxam and Tonge 1995, Germano and Bishop 2009, Escobar et al. 2010). Recent studies, however, suggest behaviors in these taxa may be more complex than previously recognized (Roe et al. 2010, Burghardt 2013, Hammond et al. 2021). Comparing habitat use of captive-reared and wild individuals can provide valuable insights into whether captive-rearing affects post-release habitat selection which can affect survival of reintroduced animals and success of reintroduction designs (Seddon et al. 2007, Roe et al. 2010, Tetzlaff et al. 2018).

Habitat use includes the diversity of macro- and microhabitats used by a species as well as how use varies over space and time (Roe and Georges 2007, Matthews and Preiser 2010, Stadtmann and Seddon 2020). Determining these relationships can be particularly important in streams because of the high degree of temporal and spatial variability that often characterizes these systems (Kupferberg 1996, Dong et al. 2016, Cecala et al. 2018). Temporally, hydrographs and hydroperiods vary across years and seasons depending on climate, weather, and sometimes human activities (Bonada et al. 2006). Spatially, streams are a nested hierarchy of physical habitats, each of which depends on larger-scale processes (Frissell et al. 1986, Cecala et al. 2018). Flow and sediment transport processes create and maintain typical stream habitats like pools, riffles, and cascades (Hawkins et al. 1993, Thomson et al. 2001). As flows change temporally, the characteristics of the habitats also change. For example, a geomorphic cascade may behave as a cascade at high water and a series of pools at low water. Habitats present at a particular time may be viewed as seasonal units. Given all of these sources of variation, understanding habitat selection at multiple temporal and spatial scales is critical for designing successful reintroductions of endangered species to stream habitats.

Reintroductions are being considered to recover the federally endangered (USFWS 2014) Sierra Nevada yellow-legged frog (Rana sierrae, MYLF ITT 2018). *R. sierrae* was once one of the most abundant and widespread amphibians in the Sierra Nevada mountains of California, USA (Grinnell and Storer 1924). It has disappeared from >90% of historical localities (Vredenburg et al. 2007) and an estimated 50% of watersheds where reproduction was documented before 1990 (Brown et al. 2014). *R. sierrae* has been well studied in high elevation lakes (Knapp et al. 2003, Matthews and Preiser 2010), but the applicability of these results to streams is poorly known. *R. sierrae* is highly aquatic at all life stages, has most commonly been found in lakes, and its multi-year tadpole stage requires permanent water that does not freeze in winter. These characteristics suggest stream-dwelling
R. sierrae would prefer pools and be restricted to perennial streams with flows or depths sufficient to prevent freezing. The few studies on R. sierrae in streams, however, suggest more complex habitat relationships. Larger populations were found in intermittent creeks than in perennial streams in one study (Brown et al. 2020). Further, frogs used varying microhabitats in diverse streams, preferred pools in three of four streams (Brown et al. 2019), and preferred shallow, slow water which could be found in various geomorphic unit types (e.g., pools, riffles, cascades, Yarnell et al. 2019). Here, we advance our understanding of R. sierrae habitat use in streams by explicitly modeling variation in habitat selection across temporal and spatial scales and by comparing habitat selection of wild and captive-reared frogs. Although reintroductions of wild and captive-reared R. sierrae have occurred (Fellers et al. 2007, Joseph and Knapp 2018, MYLF ITT 2018), there has been no study of the behavior and habitat selection of released animals, and no comparison of habitat use between wild and captive-reared frogs. To design effective reintroduction programs for R. sierrae in streams, managers need a more complete understanding of its habitat selection across the temporal and spatial diversity of available habitats, as well as of habitat selection of captive-reared frogs.

We studied habitat selection of wild and captive-reared R. sierrae at multiple scales in four diverse streams in the Sierra Nevada, California. Our objectives were to (1) characterize the variety of streams R. sierrae uses to inform selection of potential reintroduction sites; (2) quantify habitat selection at the scales of seasonal units (pool, riffle, etc., present at the time of survey) and microhabitats (specific location of frogs) to identify selection of release locations within streams; and (3) quantify temporal and spatial variation in habitat selection as available habitat changes. We then (4) examined whether captive-reared frogs used the same habitats as wild frogs across the spatial and temporal variation of available habitat. We added additional data (years and streams) to build on prior studies by analyzing habitat use vs. availability at the three spatial scales, accounting for the diverse streams, spatial diversity, and temporal variation (high to low flows). Finally, we compared habitat selection of wild vs. captive-reared frogs as part of a population augmentation. Results from this study will inform the design of effective reintroduction programs for frogs in streams.

**Methods**

**Study streams**

We studied six occupied reaches of four streams in R. sierrae’s northern range that varied by size, hydrology, geomorphology, and frog abundance (Fig. 1; Yarnell et al. 2019). Perennial Lone Rock Creek (2.7 km) and Independence Creek (0.66 m) are low-to-moderate gradient, second- and third-order reaches (Fig. 2). Lone Rock flows through a deep valley in open forest into a recreational reservoir, is downcut with large sections of eroded banks, and beaver dams create long, deep pools, and runs. Independence flows through a meadow with multiple braided side channels, floodplains, and off-channel habitats that are inundated at snowmelt, generally dry by mid-summer, and reappear in fall from water releases from an upstream reservoir. Native and nonnative fishes were present in Independence and abundant in Lone Rock (Brown et al. 2020).

Intermittent South Fork (SF) Rock Creek and Mossy Pond Creek are small, high gradient headwater creeks with large sections that dry, usually by mid-summer (Fig. 2). South Fork Rock includes three study reaches, the headwaters of the main channel (1.0 km), SF Tributary 1 (1.2 km), and SF Tributary 2 (0.4 km). These reaches are connected in the spring, but disconnect as water dries. Fishes occasionally occur in the main channel and lower sections of SF Tributary 1, but the intermittent water limits their presence. Mossy Pond (0.9 km) is surrounded by granitic bedrock and flows from a shallow lake into a reservoir. A steep barrier prevents fish from entering the creek.

Populations were small on the perennial streams (<25 adults) and larger on the intermittent streams (≤60 adults in the SF Rock reaches, ~100–200 in Mossy Pond, Brown et al. 2020).

**Field methods**

We collected aquatic habitat use vs. available habitat data four times per active season, approximately monthly from June to October 2016 to
We quantified physical, hydrologic, and cover components at three scales. We characterized habitat at each study reach and quantified habitat selection at the seasonal habitat unit (pool, riffle, cascade, etc., at the time of survey) and microhabitat (closest aquatic habitat to frog’s location) scales. We only collected data in wadable water, but streams were usually wadable. In spring 2017, high flows impeded early-season surveys at the perennial streams.

At the reach scale, we measured water stage using Solinst pressure transducers, programmed to collect data every 15 min, installed near the downstream end of each reach. In spring 2016, we mapped and classified the geomorphic units of each reach as cascade, bedrock chute, high gradient riffle, low gradient riffle, run, pool, step pool, or wood-formed pool. This classification of the individual geomorphic units did not change appreciably during the study.

Fig. 1. Locations of Rana sierrae study streams in the northern Sierra Nevada, California.
For available habitat, we established permanent transects on each reach perpendicular to the channel. We chose permanent transects rather than a case-control design (collection of data at random points near frog locations, Manly et al. 2002) to more systematically quantify changes in available habitat across the active season. We used a systematic random design meaning we used a random start point and distributed transects evenly along the reach proportional among geomorphic unit types. We aimed to sample 5–7 points on average per transect each survey and only collected data at transects with water. Using a systematic random design, we measured habitat at points along each transect spaced 0.25–1 m based on wetted width of the transect at the time of survey. In the intermittent streams, many transects dried over the active seasons; thus, we added transects in 2018 to increase the sample size of available habitat. We dropped transects in the perennial streams to balance the workload.

At each point along the transects, we recorded water depth and, in water too shallow to measure velocity (depths <0.06 m), presence/absence of visible flow. In depths ≥0.06 m, we measured water velocity using a Marsh-McBirney flow meter. We used the combination of velocity measurements from deeper water and presence of visible flow in shallow water to create a variable reflecting presence/absence of visible flow for the entire dataset. We estimated the percentage of herbaceous and total cover in a 1-m² plot centered on the point and <1 m above the stream. Total cover included anything large enough to hide a 2 cm animal (e.g., substrate, vegetation, woody debris). At each point, we visually estimated the percent of overhead canopy cover (0, 0–25, 25–50, 50–75, 75–100) which we treated as an ordinal variable and recorded substrate type (silt/organics = <0.06 mm, sand = 0.06–2 mm, fine gravel = 2–32 mm, coarse gravel = 32–64 mm, cobble = 64–256 mm, boulder = >256 mm, bedrock). We categorized substrate as silt, sand/fine gravel/coarse gravel, cobble/boulder, and bedrock. Finally, at each transect, we recorded the type (using geomorphic unit definitions, Hawkins et al. 1993) and dimensions (maximum width, maximum depth) of the seasonal habitat unit (hereafter, “seasonal unit”).

For habitat used, we surveyed approximately two passes of each stream over a ~4-d period each visit. We searched banks and all wadable water for frogs, including channels, mouths of tributaries, side channels, backwaters, and floodplains. We began surveys after 09:30 and started in different locations on each pass. For each frog, we recorded life stage and collected habitat data at its location when found in the water or at the closest water it faced when found out of water. We recorded the frog’s location as main channel, side channel, floodplains, or other, whether it was in or out of water, and the distance it was from the water’s edge. We recorded hydrologic metrics (water depth, presence/absence of visible flow, water velocity for depths ≥0.06 m), cover metrics (herbaceous, total, canopy, substrate),

Fig. 2. *Rana sierrae* study streams were diverse first- to third-order streams in their northern range. Perennial streams (a) retained a diversity of habitats while intermittent streams (b) dried to a few pools over the summer.
and the type and dimensions (maximum width, maximum depth) of the seasonal unit using the same methods as available habitat.

Our sample included 11,237 available habitat data points, and 1011 wild adult, 311 wild subadult, and 178 captive-reared use data points.

Captive rearing and frog release

We collected tadpoles from SF Rock in 2016 that were reared into adults at the San Francisco Zoo and Gardens (Brown et al. 2020). We released 22 frogs on 18 July 2017 divided evenly among two pools on each of the two SF Rock tributaries. We released 60 frogs on 5 July 2018 divided evenly among three pools on the main channel and SF Tributary 1 and two pools on SF Tributary 2. We chose the release pools based on water presence in mid-October and wild frog presence in 2016.

Analysis

Hydrologic stream flow index definition.—Stream habitats were highly dynamic, varying among years and within summers due to stream flow fluctuations. Annual precipitation varied among years with 1 April snowpacks 94% of normal in 2016, 148% of normal in 2017, and 46% of normal in 2018 (http://cedc.water.ca.gov/snowapp/sweq.action). Flows decreased over the summer and large sections of the intermittent streams dried. To account for the different annual and seasonal flow conditions, we created a hydrologic index that reflected high, medium, or low flows. We assigned each survey to one of the three categories and, for this particular metric, used different methods for perennial and intermittent streams. For perennial streams, we used stream stage based on hydrographs from the loggers, where high was flood stage, low was stage at base flow, and medium was intermediate between the two. Stage was not a good indicator for the intermittent streams; loggers were located in pools that were, to some extent, buffered from the decreasing flows over the summer. Thus, for the intermittent streams, we defined categories reflecting water retention using the percentage of transects that had water (high flows = >60%, medium flows = 30–60%, low flows = <30%). We examined habitat use across these different hydrologic index categories.

Reach scale characterization.—We plotted stage height over time for each stream and year (2017, 2018) where available. For each reach, we summed the lengths of geomorphic unit types. For further analysis of the seasonal units, we collapsed the types into three categories, cascades (cascades, chutes), riffles (high and low gradient), pools (all other categories). We included runs with pools because in the streams where these were prevalent, they were more similar to pools than riffles. We described graphically the dimensions of each reach by seasonal unit type and hydrologic index using maximum widths and depths of seasonal units, and the maximum velocity (maximum of transect points) at each transect. We calculated the percentage of each substrate type by seasonal unit type for each reach. To quantify the desiccation of the intermittent reaches, we calculated the percentage of transects with water for each survey each year. Finally, we compared the percentage of seasonal unit type by geomorphic unit type across hydrologic index categories for each reach. Based on these reach scale characteristics, we collapsed the three SF Rock reaches for the habitat selection analyses.

Habitat selection analyses.—We first used generalized linear models to examine whether frogs preferred specific geomorphic and seasonal habitat types across the different hydrologic index categories while accounting for the diverse streams. We modeled the probability of selected vs. available habitat as the response and habitat type (geomorphic or seasonal unit), hydrologic index (high, medium, or low), and stream as the predictors (SAS 9.4/Glimmix; SAS Institute Inc., Cary, North Carolina, USA). Sample sizes were too small to model the three-way interaction among habitat type, hydrologic index, and streams so we only included the three two-way interactions. Model results were similar between the geomorphic and seasonal habitats so we used seasonal unit types for further analyses; this is the habitat experienced by the frog.

We then compared selected vs. available habitat variables at the seasonal unit and microhabitat scales using a Bayesian implementation of a generalized linear mixed model with binomial probability distribution. Specifically, we used a hierarchical random slope model to examine selection of seasonal unit dimensions (maximum
wetted width, maximum depth), hydrologic factors (water depth, presence of visible flow, velocity), and cover (total, herbaceous, canopy, and substrate type). We included random slope terms for each of these predictor variables to allow selection coefficients to vary across the different seasonal units, hydrologic index categories, and streams. As an exploratory analysis, we used descriptive statistics and generalized additive models (GAM) to examine correlation among variables and to select the best functional parametric form for each predictor variable. Because the maximum Pearson’s correlation coefficient was <0.7 for all variables, no variables were excluded, and GAMs indicated that no polynomial terms were warranted. Finally, we standardized and rescaled all continuous predictor variables to have a mean of zero and a standard deviation of one.

As our study is of an endangered amphibian, our sample was small and unbalanced, with more available sample points relative to frog use points in the perennial streams and fewer available sample points relative to frog use points in the intermittent streams. This limited our ability to model the full suite of interactions among the seasonal unit types and hydrologic index categories that might affect microhabitat selection. Exploratory analyses indicated that, because our streams are diverse, the averaging effect of combining categories (e.g., streams, seasonal units, hydrologic index) obscured important variation. To solve this, we created a random factor that had 36 potential values combining the three seasonal units, three hydrologic index categories, and four streams. We then used this random factor in a hierarchical model with a random slope that allowed the relationships between the probability of use and the habitat predictors to vary among the 36 categories. This in turn allowed us to explore how habitat selection varied among seasonal units across the hydrologic index categories while accounting for the diverse streams. Further, this approach not only reduced the number of parameters estimated but allowed us to “borrow” from categories with more data to make inferences for categories with sparse data. In our interpretation of results, we are transparent about sample sizes, focus on broad patterns and defensible differences, and emphasize categories with larger sample sizes. The general model was structured as follows:

\[ Y[i] \sim \text{Binomial}(p_i, N_i) \]
\[ \logit(p_i) = \alpha_0 + \alpha_1 \text{[year[i]]} + \alpha_2 \text{[compositeRE[i]]} + \beta \text{[compositeRE[i]]} \times \mathbf{X}[i] \]

where \( Y \) indicates whether the \( i \)th observation is from used vs. available habitat measurements. We modeled a mean population intercept, \( \alpha_0 \), a varying intercept of year, \( \alpha_1 \), and varying intercepts and slopes, \( \alpha_2 \) and \( \beta \), respectively, for the composite random factor (accounting for seasonal units, hydrologic index, and stream). \( \mathbf{X} \) is a model matrix wherein columns are additive habitat variables; maximum width and maximum depth are seasonal unit scale variables; the remainder reflect microhabitats:

- Maximum depth of seasonal unit + maximum width of seasonal unit + water depth at microhabitat + presence of flow (yes/no) + % total cover + % herbaceous cover + % canopy cover + substrate.

Models were fit using diffuse, normally distributed priors for varying intercepts and slopes:

\[ \alpha_1 \sim \text{Norm}(0, \sigma_{\alpha_1}^2) \]
\[ \alpha_2 \sim \text{Norm}(0, \sigma_{\alpha_2}^2) \]
\[ \beta \sim \text{Norm}(\mu_{\beta}, \sigma_{\beta}^2) \]

Models were fit with 20,000 total iterations and 1000 iterations discarded as burn-in. We assessed convergence by examining Gelman-Rubin statistics and traceplots. Gelman-Rubin statistics were ~1 for all models. We assessed model fit using Bayesian \( R^2 \) and posterior predictive checks based on sums of squares (Kery and Royle 2016, Gelman et al. 2019). Bayesian \( R^2 \) ranged from 0.37 to 0.63 and Bayesian \( P \)-values for goodness of fit ranged from 0.10 to 0.59, both indicating adequate model fit. Models were run with JAGS using the jagsUI package to interface with R (R Core Team 2018).

Because we did not use a case–control design where use and available points were matched, we developed separate models to compare sub-
groups rather than, for example, comparing wild vs. captive-reared frogs within a single model. Thus, we developed separate models for wild adults and subadults on main channels at all streams. We developed models (separately for adults and subadults) for side channels at Independence since these were only present at this stream and their habitats were quite different than the main channel. Finally, we developed a model for captive-reared frogs at SF Rock. Because our primary interest was in assessing the relative importance of the different habitat variables for each subgroup, we compared selection coefficients within a single model, as is the common approach with Bayesian hierarchical models (Kery and Royle 2016) rather than a comparison of models representing a priori hypotheses (Burnham and Anderson 2002). We present posterior population mean estimates for coefficients of predictor variables. However, because our primary study objectives were to explore spatial and temporal variability in habitat use, we also focus on variability among the random factor categories. In our presentation of model results, we further this objective by synthesizing output from the subgroup models organized by the function of the predictor variables (seasonal unit dimensions, hydrologic, cover) rather than by models (i.e., all variables from a single model).

Up to a third of our non-edge data points (available = 30%, use = 24%) were in depths shallower than the Marsh-McBirney flow meter could measure. Our exploratory analysis suggested there was an interaction between water depth and both visible flow presence and velocity. Thus, our primary models were additive and included visible flow presence as a predictor. We then developed models further exploring the interaction of water depth with visible flow presence and the absolute value of velocity. Models with velocity only included data where depths were \( \geq 0.06 \) m.

**Results**

**Reach scale characterization**

Hydrographs of our study reaches were typical of Sierra Nevada streams with most precipitation from winter snowpacks (Appendix S1: Fig. S1). Flows were high during spring and declined through summer. High snowpacks in 2017 led to later spring runoff and higher flows later than the other years. These high flows flooded much of the off-channel habitat at Independence well into the summer.

Geomorphology varied among the study streams (Appendix S1: Fig. S2). The perennial Lone Rock had mostly pools and runs with a few steep cascades and low gradient riffles, whereas Independence was mostly riffles and pools. The intermittent Mossy Pond was dominated by cascades and chutes, whereas cascades, pools, and riffles occurred in the South Fork reaches.

The streams were relatively small, with wetted widths averaging 2.4–6.3 m (Appendix S1: Table S1, Fig. S3). In general, the intermittent streams were slightly narrower, shallower, and had slower flow than the perennial streams. South Fork Tributary 1 had a few deep pools, and its average maximum depth was almost twice that of the other intermittent reaches; its median, however, was similar. Substrate varied by reach more than by habitat type (Appendix S1: Fig. S4). Lone Rock was the most diverse reach; its cascades had more boulders, riffles more gravel, and pools more sand. Independence was dominated by cobble and boulders, Mossy Pond by bedrock and boulders, and the SF Rock reaches by boulders and bedrock.

As flows decreased, wetted widths, depths, and velocities decreased in all streams (Appendix S1: Fig. S3). Intermittent streams dried to a low of 3–30% of transects (Appendix S1: Fig. S5). As flows decreased, the habitat types available to frogs remained relatively consistent in the perennial streams, but in the intermittent streams, both the amount and type of habitat changed (Appendix S1: Fig. S6). Riffles and cascades tended to dry out or change to pools. Thus, only a few pools comprised the available habitat in the intermittent reaches for much of the active season.

**Habitat selection**

Sixty percentage of frog sightings were in water, and the remaining were on shore or on emergent objects (e.g., boulders, logs). All but three frog sightings were within 1 m of water, with a maximum of 3 m. Only Independence and Lone Rock had available aquatic habitats off the main channels. At Independence in the
high-water year 2017, all frog sightings except one were in off-channel pools, floodplains, or side channels (Appendix S2: Fig. S1a). In 2016 and 2018, all frog sightings were in the main channel and in side channels with tadpoles; the other side channels and off-channel habitat were dry for most of the summer. In the drier years, 59% of adults were found in the main channel whereas 74% of subadults were found in the breeding side channels. At Lone Rock, a few frogs (11 subadults and small adults) were found in the few off-channel pools that formed on floodplains early in the season. In the intermittent streams, frogs tended to cluster around remaining pools as the streams dried (Appendix S2: Fig. S1b). Other than these patterns, frogs did not appear to select particular areas of the streams.

Wild adults.—1. Seasonal units.—Wild adults were found in all habitat types on all streams, but they preferentially selected some specific habitats. At Lone Rock at low water, for example, similar numbers of adults were found in pools as riffles, but pools comprised 86% of the available habitat; at SF Rock at high water, similar numbers of adults were found in cascades as pools, but cascades comprised 59% of the habitat. Accounting for available habitat, wild adults did not prefer pools in the perennial streams but did prefer pools in the intermittent streams (Fig. 3). On Lone Rock during low flows, the estimated probability of use was highest in riffles, then cascades, and smallest in pools (Fig. 3). Conversely, there was no difference in the estimated probability of use among habitat types in the main channel at Independence. In the side channels of

Fig. 3. Comparison of probability of use among seasonal unit types for wild and captive-reared Rana sierrae adults across high, medium, and low hydrologic index categories in four study streams. Indep., Independence; N, number of frogs found per hydrologic index category per stream. Separate models were run for captive-reared vs. wild frogs and main vs. side channels; see Habitat selection analyses for explanation. Results for subadult models are shown in Appendix S3: Fig. S1. Adults were found in all seasonal unit types, but selected pools in the intermittent streams and riffles at low flows at Lone Rock.
Independence, the estimated probability of use by wild adults was slightly higher in riffles. In the intermittent streams, the estimated probability of use was highest in pools.

Overall, the estimated probability of use for wild adults was negatively associated with maximum wetted width of seasonal units (Table 1), though this association was most significant in pools and cascades on intermittent streams (Fig. 4; Appendix S2: Fig. S2). Although the estimated population mean coefficient for maximum water depth was not significant (Table 1), this resulted from opposing trends in intermittent and perennial streams. The estimated probability of use for wild adults was associated with shallower pools in the perennial streams and deeper pools in the intermittent streams (Fig. 4; Appendix S2: Fig. S2). There were no major associations between estimated probability of use and seasonal unit dimensions for wild adults in Independence side channels (Table 1, Fig. 4).

2. Microhabitat.—Wild adults appeared to avoid fast, deep water, particularly in the perennial streams, but otherwise, they preferred the presence of visible flow and, in the intermittent streams, deeper water. Using an additive model with the full dataset, the estimated probability of use was positively associated with the presence of visible flow in most streams and habitats (Table 1, Fig. 5). The estimated population mean

| Table 1. Population mean coefficients from random slope generalized linear models for wild and captive-reared *Rana sierrae* adults and wild subadults in four study streams. |
|---------------------------------|------------------|------------------|------------------|------------------|
| Variable                        | Main channel     |                  | Side channels    |                  |
|                                 | Wild             | Captive-reared   | Independence     |                  |
|                                 | Mean 95% CI      | Mean 95% CI      | Mean 95% CI      |
| Adults                          |                  |                  |                  |
| Intercept (no visible flow, silt)|−4.66 −7.39 to −1.98|−9.71 −18.25 to −1.66|−5.49 −11.29 to 0.04|
| Seasonal unit dimensions        |                  |                  |                  |
| Maximum wetted width            |−0.69 −1.08 to −0.31|−1.15 −1.73 to −0.52|−0.14 −0.86 to 0.62|
| Maximum water depth             |0.14 −0.34 to 0.59|0.91 −0.06 to 1.80|0.33 −0.58 to 1.29|
| Hydrologic characteristics      |                  |                  |                  |
| Water depth                     |0.42 −0.01 to 0.84|0.91 0.27 to 1.66|0.00 −0.89 to 0.77|
| Visible flow presence           |1.28 0.57 to 2.00|1.35 0.10 to 3.48|2.05 0.63 to 3.69|
| Cover                           |                  |                  |                  |
| Total                           |0.38 0.18 to 0.57|0.44 −1.59 to 2.14|0.49 −0.19 to 1.10|
| Herbaceous                      |−0.27 −0.56 to −0.00|−0.49 −1.63 to 0.13|−0.93 −1.85 to −0.18|
| Canopy                          |0.16 −0.08 to 0.38|0.38 −0.18 to 0.84|0.11 −0.35 to 0.54|
| Sand/gravel substrate           |0.05 −0.94 to 0.88|1.70 −0.57 to 3.94|−1.58 −3.62 to −0.15|
| Cobble/boulder substrate        |0.12 −0.57 to 0.80|0.24 −1.21 to 1.50|−0.40 −1.95 to 1.03|
| Bedrock substrate               |0.35 −0.66 to 1.48|0.46 −1.66 to 2.09|24.04 −0.34 to 65.46|
| Subadults                       |                  |                  |                  |
| Intercept (no visible flow, silt)|−6.98 −10.74 to −3.47|−0.25 −17.72 to −2.34|
| Seasonal unit dimensions        |                  |                  |                  |
| Maximum wetted width            |−1.12 −1.95 to −0.39|−0.58 −3.08 to 1.67|0.66 −1.87 to 3.77|
| Maximum water depth             |−0.02 −0.69 to 0.57|                  |                  |
| Hydrologic characteristics      |                  |                  |                  |
| Water depth                     |0.54 −0.15 to 1.23|1.15 −0.68 to 2.47|−0.41 −3.68 to 3.21|
| Visible flow presence           |0.80 −0.61 to 2.18|                  |                  |
| Cover                           |                  |                  |                  |
| Total                           |0.24 −0.22 to 0.64|0.18 −2.03 to 2.57|
| Herbaceous                      |−0.22 −0.78 to 0.21|0.12 −2.03 to 2.38|
| Canopy                          |−0.34 −0.61 to −0.08|−0.31 −2.00 to 1.21|
| Sand/gravel substrate           |−1.30 −3.59 to 0.39|−2.03 −9.56 to 4.07|
| Cobble/boulder substrate        |−0.55 −1.99 to 0.85|−2.70 −9.64 to 0.35|
| Bedrock substrate               |0.00 −1.98 to 2.10|−2.68 −66.43 to 59.31|

Note: Bold italicized coefficients indicate 95% credible intervals do not overlap 0.
The coefficient for maximum water depth was not significant (Table 1), but there was variability between intermittent and perennial streams. The estimated probability of use of wild adults was either negatively or not associated with water depth in the perennial streams, and positively associated with water depth in the intermittent streams. However, the interaction models with water depth × presence of visible flow (full data set) and water depth × velocity (depths ≥0.06 m) showed more complex relationships. Using the water depth × presence of visible flow model, the estimated probability of use for wild adults was positively associated with water depth where visible flow was not present (Fig. 6a; Appendix S2: Figs. S3, S4). In the presence of visible flow, the estimated probability of use was negatively associated with water depth in perennial streams (Fig. 6b; Appendix S2: Fig. S3) and varied by habitat type and reach in intermittent streams (Fig. 6b; Appendix S2: Fig. S4). Similarly, using the depth × velocity model, the estimated probability of use was negatively associated with water velocity in the perennial streams, and varied by habitat type and stream in intermittent streams (Fig. 7; Appendix S2: Fig. S5).

Wild adults had weak associations with the cover variables. The estimated population mean coefficient was positive for total cover, negative for herbaceous cover, positive but non-significant for canopy cover, and non-significant for substrates (Table 1, Fig. 8; Appendix S2: Fig. S6).
Captive-reared adults.—1. Seasonal units.—Most SF Rock captive-reared adults were found in pools and the estimated probability of use was highest in pools (Fig. 3). We released frogs into pools, and they tended to stay. Similar to wild adults, the estimated probability of use of captive-reared adults was negatively associated with maximum wetted width and positively associated with maximum water depth of seasonal units (Table 1, Fig. 4; Appendix S2: Fig. S2).

2. Microhabitat.—Captive-reared adults showed the same general flow and water depth preferences as wild adults in SF Rock (Table 1, Fig. 5; Appendix S2: Figs. S4, S5). The estimated population mean coefficients were not significant for the cover variables (Table 1). However, when comparing the variability among seasonal units and the hydrologic index, the relationships generally were similar to wild SF Rock adults (Fig. 8; Appendix S2: Fig. S6).

Wild subadults.—1. Seasonal units.—Overall, wild subadults selected similar seasonal unit types as wild adults, though the preference for riffles in Lone Rock was more evident (Appendix S3: Fig. S1). Subadults tended to be found in more narrow and shallower seasonal units in the perennial streams, except that they preferred deeper riffles at low water at Lone Rock (Table 1; Appendix S3: Figs. S2, S3). In Mossy Pond, subadults shifted from using narrow and deeper pools at high and medium flows to wider and shallower pools at low water. The same general pattern occurred at SF Rock but to a lesser degree.
Fig. 6. Examples of estimated relationships between habitat use and water depth (a) without and (b) with the presence of visible flow in pools, riffles, and cascades in perennial (Independence) and intermittent (South Fork [SF] Tributary 1) streams for wild adult *Rana sierrae*. Estimated relationships are based on models with interaction terms for water depth and the presence of flow using the entire dataset. Blue lines are high water, yellow medium water, and red low water. Dotted lines are 95% credible intervals. Faded lines are categories with low sample sizes (*N* < 5). Water depth × flow model results differed among the SF Rock reaches, shown for all streams for adults in Appendix S2: Figs. S3, S4 and for subadults in Appendix S3: Figs. S4, S5.
2. Microhabitat.—Wild subadults showed similar flow and water depth preferences as wild adults (Table 1; Appendix S3: Figs. S2, S4–S6), with the exception that in Independence side channels, they tended to be in deeper water and no visible flow presence (Appendix S3: Fig. S2). There were few strong associations with subadult use and cover, though the estimated population mean coefficient for canopy cover was significantly negative (Table 1; Appendix S3: Fig. S7).

**DISCUSSION**

Understanding the breadth of habitat selection at multiple spatial and temporal scales for both wild and captive-reared animals can lead to more successful reintroduction strategies (Cochran-Biederman et al. 2015, Zhang et al. 2017, Stadtmann and Seddon 2020). This may be particularly true for stream-dwellers whose available habitats change across space and time (Yarnell 2013, Dong et al. 2016, Cecala et al. 2018). Our study suggests that *R. sierrae* is an aquatic generalist (Cabral Eterovick 2003, Sredl and Jennings 2005) at multiple spatial scales. Frogs appeared able to meet their ecological requirements in a variety of habitats, with some site-specific constraints affecting habitat selection. Our results suggest that understanding how annual and seasonal flow patterns affect available habitats is key to selecting reintroduction streams. Finally, captive-rearing did not appear to alter habitat selection, supporting the use of wild frog habitat preferences to develop reintroduction designs and suggesting simple releases may be sufficient.

*Rana sierrae*’s use of diverse stream habitats is most apparent at our largest scale—the stream. *R. sierrae* was found in streams that ranged from first to third order, high to low gradient, occurred in open forest or meadows, included both perennial and intermittent waters with fast-flowing and still-water, and differed geomorphologically. Intermittent streams in the study were similar to those described by early studies of *R. sierrae* (Zweifel 1955, Mullally and Zweifel 1955, Mullally and Zweifel 1955).
Cunningham 1956) and to those used by the closely related *Rana muscosa* in southern California (Mullally 1959, Santana 2012).

The use of small intermittent streams by such a highly aquatic frog like *R. sierrae* may seem counterintuitive. Nonetheless, others have reported higher abundances in intermittent creeks than in perennial streams (Mullally and Cunningham 1956, Brown et al. 2020), emphasizing the importance of these headwater habitats (Olson and Weaver 2007, Richardson and Danehy 2007). Across its broader range, *R. sierrae* commonly uses lentic waters (Knapp et al. 2003), habitats akin to pools of intermittent streams (Cabral Eterovick 2003). Frogs appeared to survive in intermittent streams by moving to the few persistent pools as water dried, including moving long distances (Mullally and Cunningham 1956, Mullally 1959, Keung et al. 2021). Populations in these streams may be vulnerable during droughts, and it is unknown whether *R. sierrae* can withstand total desiccation of their habitats like some Ranid frogs in arid environments (Hinderer et al. 2021). The absence of fish, a known cause of declines for *R. sierrae* (Knapp and Matthews 2000), may contribute to the higher abundances in the intermittent streams. Nonnative trout now occur in almost all perennial streams in the species’ range. The current populations in intermittent streams may be remnants of formerly larger populations in downstream perennial reaches before the introduction of fishes (Brown et al. 2020). Regardless of the species’ historical use of intermittent streams,
given current conditions, these creeks may provide refuge from fishes and merit appropriate management.

At the seasonal unit scale, we predicted that wild frogs would prefer deep pools based on assumptions from *R. sierrae* in lakes. Frogs did prefer deeper pools in the intermittent streams which, by retaining more water during dry periods, were the primary habitat available most of the summer. This was similar to *R. muscosa* in southern California streams (Santana 2012). Surprisingly, *R. sierrae* also used cascades and riffles in the intermittent streams when available. In the perennial streams, frogs did not prefer pools relative to availability. Pools may have been the least safe habitats in these streams because of the presence of fishes. Lone Rock, in particular, had large numbers of both native and nonnative fishes and the sandy substrate of the long deep pool runs provided little cover. Fish presence also may explain the frogs’ preference for shallower seasonal units in the perennial streams (Hunter and Smith 2013). The fast flow of riffles in the perennial streams or deep water of pools in the intermittent streams may facilitate quick escape from predators (Gillespie and Hollis 1996). We observed frogs escaping into fast-flowing water as well as taking cover at the bottom of deep pools. Also, higher periphyton growth in riffles and cascades can lead to more emerging macroinvertebrate prey (McKie et al. 2018), possibly increasing use of these habitats. This behavioral flexibility may allow *R. sierrae* to adjust at this scale to site-specific opportunities and constraints like prey availability, fish predation, and seasonal desiccation of habitats (Cabral Eterovick 2003).

At the microhabitat scale, we predicted that frogs would prefer deep water with low or no flow, again based on assumptions from *R. sierrae* in lakes. Frogs generally did avoid high velocity deep water, which may be difficult to navigate. This may explain the shift to off-channel habitats at Independence and use of floodplain pools by subadults at Lone Rock during high flows. This generally agrees with Yarnell et al. (2019) who found that frogs preferred shallow and low velocity water, which they find in a variety of geomorphic unit types. Our analyses add nuance to this result, however, by using a random slope model that explicitly accounted for habitats available at the time of survey (seasonal units), flows (hydrologic index), and streams, and by explicitly modeling the interaction between depths and flow (presence and water velocity). Overall, our model found frogs more often in water with visible flow and deeper water where flow was not visible. Supporting these results, we commonly found frogs basking next to cascades or riffles, in pools at the bottom of cascades, on rocks in shallow water trickles or sheetflow, and occasionally in the spray zone behind small waterfalls. These areas may provide moist foraging habitat or help with thermoregulation (Gillespie and Hollis 1996). In addition, frogs used flowing water to escape, and we observed no signs that frogs avoided or were not able to navigate flowing water.

*Rana sierrae* showed some preference for areas with higher total cover, but not specifically for cover associated with herbaceous vegetation or specific substrates like silt, cobble, and boulders. This differs from many amphibian species like giant salamanders (Bodinof et al. 2012, Zhang et al. 2017), tailed frogs (*Ascaphus truei*, Adams and Bury 2002), and *Leiopelma hochstetteri* (Nájera-Hillman et al. 2009) which are all strongly associated with cobble and boulders that provide protective cover. Stream-dwelling *Rana luteiventris* (Arkle and Pilliod 2015) and *Lithobates chiricahuensis* (Hinderer et al. 2021) were associated with emergent vegetation. In contrast with these species that have clear affinities with specific cover types, *R. sierrae* showed behavioral flexibility in their use of cover.

Finally, whether captive-reared animals develop behaviors that are deleterious in the wild can affect the success of a reintroduction program (Seddon et al. 2007, Germano and Bishop 2009, Santos et al. 2009). Captive-reared frogs released into an intermittent stream exhibited the same behavioral flexibility as wild frogs from the same stream. Not only did they select similar habitats as wild frogs as shown here, they also have been shown to exhibit similar movement distances (Keung et al. 2021). Behavioral flexibility in both habitat selection and movements may help reintroduced animals stay in release habitats as well as acclimate to changing habitats (Cabral Eterovick 2003, Santos et al. 2009, Keung et al. 2021). Our results add to a small but growing number of studies that...
indicate captive-reared amphibians tend to retain natural behaviors (Germano and Bishop 2009, Berger-tal et al. 2020, Roznik and Reichling 2021).

The results here suggest that soft releases or behavioral acclimation may not be necessary for reintroductions of *R. sierrae* or similar species in streams. However, our still-water release pools likely were similar hydrologically to the aquarium environments where the captive frogs were reared (Burghardt 2013). Whether frogs released into fast-water riffles or cascades would show similar behaviors or benefit from conditioning remains unknown. We also purposefully released frogs in small groups into pools that had been occupied by wild frogs, assuming this reflected high-quality habitat. Whether this may have influenced the behavior of the captive-reared frogs merits further study. In other taxa, releasing animals with conspecifics may help them stay in release habitats (Lloyd et al. 2019). Anecdotally, we found that frogs left one release pool earlier than frogs released into other pools. Understanding whether such behaviors were related to habitat quality, competition with resident wild frogs, or behaviors such as exploration and kin aggregation would inform effective reintroduction designs (Blaustein et al. 1984, Bell et al. 2004, Hammond et al. 2021).

Ultimately, factors that contribute to reintroduction success are complex, and long-term monitoring may help elucidate whether our results are consistent long-term and their applicability to other systems (Roe et al. 2010, 2015).

**Candidate streams for reintroductions**

*Rana sierrae* appears able to meet its ecological requirements in a variety of habitats. Thus, while we have extensively quantified habitats at multiple scales (also Brown et al. 2019), we suggest these relationships be used as guidance and not prescriptive, and caution against using simple habitat suitability cutoffs to make specific management and conservation decisions (Cecala et al. 2018). While our results provide such guidance for identifying candidate reintroduction streams, we do not show data for breeding or overwintering habitats, two components critical for population persistence that warrant further study (Brown et al. 2019). Importantly, our study suggests that release designs can be based on wild frog habitat preferences.

Ideal candidate reintroduction streams would have suitable habitat present across appropriate spatial and temporal scales (Stadtmann and Seddon 2020). For both perennial and intermittent streams, understanding how available habitat changes both annually and seasonally is critical, including across both wet and dry years.

Our results suggest candidate streams may include a broad array of first- to third-order stream types (Mullally and Cunningham 1956, Brown et al. 2019). At a minimum, streams need permanent water, though this may be continuously flowing in perennial streams or patches on intermittent streams. Ideal candidate streams would be fish-free, although small populations of frogs coexist with fish on several study streams. Although reintroducing frogs to intermittent streams may seem counterintuitive for this highly aquatic species, they may provide important fish-free refuge.

Although reaches with numerous deep pools that retain water through summer seem an intuitive choice, this presumed lentic species also used non-pool habitats when available. The presence of fish also may influence habitat selection at the within-stream scale. Thus, streams with a mix of seasonal unit types (pools, riffles, cascades) that include permanent water refuges may be optimal (Yarnell 2013, McCoy et al. 2014). *R. sierrae* displacement distances (likely while streams had water) can provide guidance on spatial configurations of permanent water patches that the species may be able to tolerate. On intermittent streams, average maximum displacement distances of wild frogs ranged from 36 to 84 m with a maximum of 670 m (Keung et al. 2021).

Refuge from high spring runoff flows may be important, particularly in perennial streams. In streams from the current study, this was provided by off-channel habitats in one stream and presumably on-channel habitats at the others.

At microhabitat scales, sufficient cover and basking perches are important, and for *R. sierrae*, these can take various forms. We observed frogs taking cover in silt, cobbles, boulders, undercut banks, woody debris, and fast-flowing water. Examples of basking perches included substrate of all types, wood, and shorelines.

Ideally, release sites, an important component of reintroduction designs, would provide safe, stable habitats where reintroduced frogs would
remain until acclimated (Slater and Altman 2011, Bodinof et al. 2012). For R. sierrae, these may be shallower flowing water in perennial streams with fish, and deep pools in the absence of fish and where water is limited.

In conclusion, our results provide insights for designing effective reintroduction programs for an endangered species in stream environments, taking into account spatial and temporal changes in available habitat as well as the full diversity of a species’ habitat use (Dodd and Seigel 1991, McCoy et al. 2014, Cecala et al. 2018). Reintroduction designs that take into account physical and biological constraints when selecting streams and release sites may be most effective. For stream-dwelling R. sierrae, physical constraints include changes in available habitats from early season high flows to late-season desiccation. Biological constraints include the distribution of fish predators in different seasonal units, an area that needs further research. Finally, our results suggest that captive-reared R. sierrae will likely behave similarly to wild frogs. Our results demonstrate the importance of basing reintroduction designs on the full spectrum of habitats used by a species, moving beyond general knowledge from a single or most commonly used habitat at a single point in time.

ACKNOWLEDGMENTS

The USDA Forest Service funded and supported this study. We thank the Plumas and Lassen National Forests including Colin Dillingham, Melanie McFarland, Deborah Urich, Tina Hopkins, Todd Rawlinson, Matthew Johnson, and their field crews for their support on all aspects of the study including logistics, fieldwork, and safety. We thank Roland Knapp and Sarah Mussulman for valuable suggestions on project development. We thank Sarah Mussulman, Isaac Chellman, and CDFW crews for identifying frog locations at Mossy Pond Creek. Jessie Bushell and the San Francisco Zoo successfully reared our tadpoles to adult frogs. We thank the Center for Watershed Sciences and Sarah Yarnell for administrative support. Sarah Yarnell contributed to the design and development of this study. We thank Brendan Kavanaugh for his hard work completing the project setup and initial phase. Our hard-working field crews were Cierra Scriven, Lauren Poon, Tessa Zapalac, Jake Trusheim, Corey Luna, Cynthia Pu, and Hailey Price. We conducted work under U.S. Fish and Wildlife Service Permit TE40087B-2, CA Department of Fish and Wildlife Scientific Collecting Permit SC-0304, and UC Davis Institutional Animal Care and Use Committee Protocols #20629/#19974.

LITERATURE CITED

Adams, M. J., and R. B. Bury. 2002. The endemic headwater stream amphibians of the American Northwest: associations with environmental gradients in a large forested preserve. Global Ecology and Biogeography 11:169–178.

Arkle, R. S., and D. S. Pilliod. 2015. Persistence at distributional edges: Columbia spotted frog habitat in the arid Great Basin, USA. Ecology and Evolution 5:3704–3724.

Armstrong, D. P., and P. J. Seddon. 2008. Directions in reintroduction biology. Trends in Ecology and Evolution 23:20–25.

Bell, B. D., S. Pledger, and P. Dewhurst. 2004. The fate of a population of the endemic frog Leioptelma pakeka (Anura: Leiopelmatidae) translocated to restored habitat on Maud Island, New Zealand. New Zealand Journal of Zoology 31:123–131.

Bennett, V. A., V. A. Doerr, E. D. Doerr, A. D. Manning, D. B. Lindenmayer, and H. J. Yoon. 2013. Causes of reintroduction failure of the brown tree creeper: implications for ecosystem restoration. Austral Ecology 38:700–712.

Berger-Tal, O., D. Blumstein, and R. R. Swaigood. 2020. Conservation translocations: a review of common difficulties and promising directions. Animal Conservation 23:121–131.

Blaustein, A. R., R. K. O’Hara, and D. H. Olson. 1984. Kin preference behaviour is present after metamorphosis in Rana cascadae frogs. Animal Behaviour 32:445–450.

Bloxam, Q. M. C., and S. J. Tonge. 1995. Amphibians: suitable candidates for breeding-release programmes. Biodiversity and Conservation 4:636–644.

Bodinof, C. M., J. T. Briggler, R. E. Junge, J. Beringer, M. D. Wanner, C. D. Schuette, J. Ettling, and J. J. Millspaugh. 2012. Habitat attributes associated with short-term settlement of Ozark hellbender (Cryptobranchus alleganiensis bishopi) salamanders following translocation to the wild. Freshwater Biology 57:178–192.

Bonada, N., M. Rieradevall, N. Prat, and V. H. Resh. 2006. Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. Journal of the North American Benthological Society 25:32–43.

Brown, C., N. C. Keung, C. P. Dillingham, S. Mussulman, J. Bushell, R. Sollmann, B. D. Todd, and S. P.
Lawler. 2020. Using demography to evaluate reintroductions for conservation of the endangered frog, *Rana sierrae*, in streams. Herpetologica 76:383–395.

Brown, C., L. R. Wilkinson, and K. B. Kiehl. 2014. Comparing the status of two sympatric amphibians in the Sierra Nevada, California: insights on ecological risk and monitoring common species. Journal of Herpetology 48:74–83.

Brown, C., L. R. Wilkinson, K. K. Wilkinson, T. Tunstall, R. Foote, B. D. Todd, and V. T. Vredenburg. 2019. Demography, habitat, and movements of the Sierra Nevada Yellow-legged Frog (*Rana sierrae*) in streams. Copeia 107:661–675.

Burghardt, G. M. 2013. Environmental enrichment and cognitive complexity in reptiles and amphibians: concepts, review, and implications for captive populations. Applied Animal Behaviour Science 147:286–298.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cabral Eterovick, P. 2003. Distribution of anuran species among montane streams in south-eastern Brazil. Journal of Tropical Ecology 19:219–228.

Cecala, K. K., J. C. Maerz, B. J. Halstead, J. R. Frisch, T. L. Gragson, J. Hepinstall-Cymerman, D. S. Leigh, C. R. Jackson, J. T. Peterson, and C. M. Pringle. 2018. Multiple drivers, scales, and interactions influence southern Appalachian stream salamander occupancy. Ecosphere 9:e02150.

Cheyne, S. M. 2006. Wildlife reintroduction: considerations of habitat quality at the release site. BMC Ecology 6:1–8.

Cochran-Biederman, J. L., K. E. Wyman, W. E. French, and G. L. Loppnow. 2015. Identifying correlates of success and failure of native freshwater fish reintroductions. Conservation Biology 29:175–186.

Dodd Jr., C. K., and R. A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47:336–350.

Dong, X., N. B. Grimm, K. Ogle, and J. Franklin. 2016. Temporal variability in hydrology modifies the influence of geomorphology on wetland distribution along a desert stream. Journal of Ecology 104:18–30.

Escobar, R. A., E. Besier, and W. K. Hayes. 2010. Evaluating headstarting as a management tool: post-release success of green iguanas (*Iguana iguana*) in Costa Rica. International Journal of Biodiversity and Conservation 2:204–214.

Fellers, G. M., D. F. Bradford, D. Pratt, and L. L. Wood. 2007. Demise of repatriated populations of mountain yellow-legged frogs (*Rana muscosa*) in the Sierra Nevada of California. Herpetological Conservation and Biology 2:5–21.

Frisse1, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Gelman, A., B. Goodrich, J. Gabry, and A. Vehtari. 2019. R-squared for Bayesian regression models. American Statistician 73:307–309.

Germann, J. M., and P. J. Bishop. 2009. Suitability of amphibians and reptiles for translocation. Conservation Biology 23:7–15.

Gillespie, G., and G. Hollis. 1996. Distribution and habitat of the spotted tree-frog, *Litoria spencerii* Dubois (Anura: Hylidae), and an assessment of potential causes of population declines. Wildlife Research 23:49–75.

Grinnell, J., and T. I. Storer. 1924. Animal life in the Yosemite. University of California Press, Berkeley, California, USA.

Hammond, T. T., M. J. Curtis, L. E. Jacobs, M. W. Tobler, R. R. Swaisgood, and D. M. Shier. 2021. Behavior and detection method influence detection probability of a translocated, endangered amphibian. Animal Conservation 24:401–411.

Hawkins, C. P., et al. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18:3–12.

Hinderer, R. K., A. R. Litt, and M. McCaffery. 2021. Habitat selection by a threatened desert amphibian. Ecology and Evolution 11:536–546.

Hunter, D., and M. J. Smith. 2013. Multiscale habitat assessment for the endangered booroolong frog (*Litoria booroolongensis*): implications for threatened species management in the rural landscape of southeastern Australia. Herpetological Conservation and Biology 8:122–130.

Jachowski, D. S., R. A. Gitzen, M. B. Grenier, B. Holmes, and J. J. Millspaugh. 2011. The importance of thinking big: Large-scale prey conservation drives black-footed ferret reintroduction success. Biological Conservation 144:1560–1566.

Joseph, M. B., and R. A. Knapp. 2018. Disease and climate effects on individuals drive post-reintroduction population dynamics of an endangered amphibian. Ecosphere 9:1–18.

Jule, K. R., L. A. Leaver, and S. E. G. Lea. 2008. The effects of captive experience on reintroduction survival in carnivores: a review and analysis. Biological Conservation 141:355–363.

Kery, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology. Elsevier, London, UK.

Keung, N. C., S. P. Lawler, S. M. Yarnell, B. D. Todd, and C. Brown. 2021. Movement ecology of stream-
dwellling Sierra Nevada yellow-legged frog (Rana sierrae) informs reintroductions. Herpetological Conservation and Biology 16:72–85.

Knapp, R. A., and K. Matthews. 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog (Rana muscosa) from within protected areas. Conservation Biology 4:428–438.

Knapp, R. A., K. R. Matthews, H. K. Preisler, and R. Jellison. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. Ecological Applications 13:1069–1082.

Kupferberg, S. J. 1996. Hydrologic and geomorphic factors affecting conservation of a river-breeding frog (Rana boylii). Ecological Applications 6:1332–1344.

Lloyd, N. A., N. J. Hostetter, C. L. Jackson, S. J. Converse, and A. Moehrenschlager. 2019. Optimizing release strategies: a stepping-stone approach to reintroduction. Animal Conservation 22:105–115.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Matthews, K. R., and H. Preisler. 2010. Site-fidelity of the declining amphibian Rana sierrae (Sierra Nevada Yellow-legged Frog). Canadian Journal of Fisheries and Aquatic Sciences 67:243–255.

McCoy, E., N. Osman, B. Hauch, A. Emerick, and H. Mushinsky. 2014. Increasing the chance of successful translocation of a threatened lizard. Animal Conservation 17:56–64.

McKie, B., L. Sandin, P. Carlson, and R. Johnson. 2018. Species traits reveal effects of land use, season and habitat on the potential subsidy of stream invertebrates to terrestrial food webs. Aquatic Sciences 80:15.

Mullally, D. P. 1959. Notes on the natural history of Rana muscosa Camp in the San Bernardino Mountains. Herpetologica 15:78–80.

Mullally, D. P., and J. D. Cunningham. 1956. Ecological relations of Rana muscosa at high elevations in the Sierra Nevada. Herpetologica 12:189–198.

MYLF ITT [Mountain Yellow-legged Frog Interagency Technical Team]. 2018. Interagency conservation strategy for mountain yellow-legged frogs in the Sierra Nevada (Rana sierrae and Rana muscosa). California Department of Fish and Wildlife, National Park Service, U.S. Fish and Wildlife Service, U.S. Forest Service. Version 1.0. https://www.fws.gov/sacramento/es_species/Accounts/Amphibians-Reptiles/sn_yellow_legged_frog/documents/Mountain-Yellow-Legged-Frog-Conservation-Strategy-Signed-508.pdf

Nájera-Hillman, E., A. C. Alfaro, S. O’Shea, B. Breen, N. Garret, and P. King. 2009. Habitat-use model for the New Zealand endemic frog Leiopelma hochstetteri. Endangered Species Research 9:23–31.

Olson, D. H., and G. Weaver. 2007. Vertebrate assemblages associated with headwater hydrology in western Oregon managed forests. Forest Science 53:343–355.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rantanen, E. M., F. Buner, P. Riordan, N. Sotherton, and D. W. Macdonald. 2010. Habitat preferences and survival in wildlife reintroductions: an ecological trap in reintroduced grey partridges. Journal of Applied Ecology 47:1357–1364.

Richardson, J. S., and R. J. Danehy. 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. Forest Science 53:131–147.

Roe, J. H., M. R. Frank, S. E. Gibson, O. Attum, and B. A. Kingsbury. 2010. No place like home: an experimental comparison of reintroduction strategies using snakes. Journal of Applied Ecology 47:1253–1261.

Roe, J. H., M. R. Frank, and B. A. Kingsbury. 2015. Experimental evaluation of captive-rearing practices to improve success of snake reintroductions. Herpetological Conservation and Biology 10:711–722.

Roe, J. H., and A. Georges. 2007. Heterogeneous wetland complexes, buffer zones, and travel corridors: landscape management for freshwater reptiles. Biological Conservation 135:67–76.

Roznik, E. A., and S. B. Reichling. 2021. Survival, movements and habitat use of captive-bred and reintroduced dusky gopher frogs. Animal Conservation 24:51–63.

Santana, F. E. 2012. Mountain yellow-legged frog (Rana muscosa) conservation: multiple approaches. Thesis. San Diego State University, San Diego, California, USA.

Santos, T., J. Pérez-Tris, R. Carbonell, J. L. Telleria, and J. A. Díaz. 2009. Monitoring the performance of wild-born and introduced lizards in a fragmented landscape: implications for ex situ conservation programmes. Biological Conservation 142:2923–2930.

Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. Conservation Biology 21:303–312.

Slater, G. L., and B. Altman. 2011. Avian restoration in the prairie-oak ecosystem: a reintroduction case
study of western bluebirds to San Juan Island, Washington. Northwest Science 85:223–232.
Sredl, M. J., and R. D. Jennings. 2005. *Rana chiricahuensis* (Platz and Mecham, 1979) Chiricahua Leopard Frogs. Pages 546–549 in M. Lannoo, editor. Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, California, USA.
Stadtmann, S., and P. J. Seddon. 2020. Release site selection: reintroductions and the habitat concept. Oryx 54:687–695.
Stamps, J. A., and R. R. Swaisgood. 2007. Someplace like home: experience, habitat selection and conservation biology. Applied Animal Behaviour Science 102:392–409.
Tetzlaff, S. J., J. H. Sperry, and B. A. DeGregorio. 2018. Captive-reared juvenile box turtles innately prefer naturalistic habitat: implications for translocation. Applied Animal Behaviour Science 204:128–133.
Tetzlaff, S. J., J. H. Sperry, and B. A. DeGregorio. 2019. Effects of antipredator training, environmental enrichment, and soft release on wildlife translocations: a review and meta-analysis. Biological Conservation 236:324–331.
Thomson, J., M. Taylor, K. Fryirs, and G. Brierley. 2001. A geomorphological framework for river characterization and habitat assessment. Aquatic Conservation: Marine and Freshwater Ecosystems 11:373–389.
Tuberville, T. D., E. E. Clark, K. A. Buhlmann, and J. W. Gibbons. 2005. Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). Animal Conservation 8:349–358.
USFWS [US Fish and Wildlife Service]. 2014. Endangered species status for Sierra Nevada yellow-legged frog and northern distinct population segment of the mountain yellow-legged frog, and threatened species status for Yosemite toad: final rule. Federal Register 79:24256–24310.
Vredenburg, V. T., R. Bingham, R. Knapp, J. A. T. Morgan, C. Moritz, and D. Wake. 2007. Concordant molecular and phenotypic data delineate new taxonomy and conservation priorities for the endangered mountain yellow-legged frog. Journal of Zoology 271:361–374.
Yarnell, S. 2013. Stream habitat associations of the foothill yellow-legged frog (*Rana boylii*): the importance of habitat heterogeneity. Pages 193–211 in I. Madock, A. Harby, P. Kemp, and P. Wood, editors. Ecohydraulics: an integrated approach. Wiley-Blackwell, Oxford, UK.
Yarnell, S. M., R. A. Peek, N. Keung, B. D. Todd, S. Lawler, and C. Brown. 2019. A lentic breeder in lotic waters: Sierra Nevada yellow-legged frog (*Rana sierrae*) habitat suitability in northern Sierra Nevada streams. Copeia 107:676–693.
Zhang, L., Q. Wang, S. T. Willard, W. Jiang, H. Zhang, H. Zhao, and A. J. Kouba. 2017. Environmental characteristics associated with settlement of reintroduced Chinese giant salamanders. Journal of Herpetology 51:417–424.
Zweifel, R. G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylii* group. University of California Publications in Zoology 54:207–292.

**DATA AVAILABILITY**

Data are not publicly available due to the sensitivity of the species data. Qualified researchers may obtain data from Cathy Brown, Team Leader, of the USDA Forest Service Sierra Nevada Amphibian Monitoring Team, Stanislaus National Forest (email: cathy.brown@usda.gov).

**SUPPORTING INFORMATION**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3799/full