MOVEMENT ECOLOGY STUDY OF STREAM-DWELLING SIERRA NEVADA YELLOW-LEGGED FROGS (*Rana sierrae*) to Inform Reintroductions

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Abstract.—We studied the movements of wild and captive-raised endangered Sierra Nevada Yellow-legged Frogs (Rana sierrae) to evaluate reintroductions as a recovery tool and to inform reintroduction designs. We examined movements using 3 v of capture-mark-recapture data from 2016–2018 in four streams in the northern range of the species and radio-telemetry data from 2017–2018 at one site where we released captive-raised individuals. We quantified movement rates, maximum displacement, and maximum movements, and compared capture-markrecapture results with those from radio-telemetry. Wild frogs commonly moved little within 4-d surveys (median = 3 m; interquartile range, 0–9.8 m), but some traveled farther within and across site visits (e.g., 197 m over 2 d; 1,264 m over 29 d). We found all but one frog within 1 m of water and most within the stream channel. Movement rates decreased from June to October, and in intermittent streams, many frogs moved toward persistent pools as streams dried over summer months. Captive-raised frogs moved an estimated one-quarter to one-third less than wild frogs depending on the metric. Sixty-two percent of radio-tracked captive-raised frogs remained in release pools during the first month, and 92% did not disperse > 50 m in each tracking year. Several captive-raised frogs moved > 100 m, however, based on capture-mark-recapture. Our results suggest that captive-raised frogs may settle at release sites, but can travel in response to changing environmental conditions. Our findings also suggest that understanding seasonal water availability relative to typical movement distances may aid site selection when designing effective reintroduction plans.

Key Words.—amphibian decline; captive-reared; conservation; head-start program; population augmentation; spatial ecology; stream habitat; translocation

INTRODUCTION

As amphibians decline worldwide (Wake and Vredenburg 2008), conservation approaches like reintroduction and population augmentation become increasingly important for species recovery (Dodd 2005). Amphibians may be ideal candidates for captive breeding or head-start programs due to their high fecundity, lack of parental care, low maintenance costs, and retention of ecologically appropriate behavioral and physiological traits (Bloxam and Tonge 1995). The complex life cycles of amphibians, however, combined with the potential synergistic effects of threats in the wild can limit the success of reintroductions (Scheele et al. 2014). The failure of amphibian reintroductions may result from poor-quality habitat where animals were released (Griffith et al. 1989), failure to eliminate or mitigate the initial causes of declines (Dodd and Seigel 1991; Fellers et al. 2007; Joseph and Knapp 2018), translocation stress, or high mortality associated with post-release dispersal (Dodd and Seigel 1991; Armstrong and Seddon 2008).

Understanding post-release behaviors, like movements, can help managers evaluate reintroductions as a recovery tool and design effective reintroductions (Dodd 2005; Germano and Bishop 2009). Movement studies for amphibians raised in head-start programs and released into the wild are rare, but a few examples exist. For Maud Island Frogs (Leiopelma pakeka), individuals released in their first year remained an average distance of 4.8 m from release sites, but those released the following year established themselves a significantly greater average distance of 8 m away (Bell et al. 2004). For Ozark Hellbenders (Cryptobranchus alleganiensis bishopi), released individuals displayed a short period of exploration prior to settling within 50 m of release sites

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and only after winter did released and wild individuals show similar home-range sizes (Bodinof et al. 2012). Given that movement behaviors and post-release movement can vary among species, reintroduction designs may benefit from species-specific movement data.

Reintroductions are being evaluated as a potential recovery tool for the Sierra Nevada Yellow-legged Frog (Rana sierrae; Fellers et al. 2007; Joseph and Knapp 2018; Mountain Yellow-legged Frog Interagency Technical Team [MYLF ITT] 2018), federally listed as endangered. Once abundant throughout the Sierra Nevada of California, USA (Grinnell and Storer 1924), R. sierrae distribution and abundance have greatly decreased (Vredenburg et al. 2007; Brown et al. 2014b), thereby making reintroduction an increasingly important conservation option. In general, R. sierrae has been considered a lake species and its movements and ecology have been well-studied in lakes (Matthews and Pope 1999; Pope and Matthews 2001; Matthews and Preisler 2010). Stream habitats, however, are also important to this species, particularly in its northern range where populations have declined the most (Brown et al. 2014a; MYLF ITT 2018; Brown et al. 2019, 2020; Yarnell et al. 2019). Only two published studies have examined the success of R. sierrae reintroductions (Fellers et al. 2007; Joseph and Knapp 2018). Both studies focused on survival of animals after release and on the potential causes of population declines. Both studies were conducted in lakes, with neither addressing stream movements. Few have studied the movements of R. sierrae in streams (Brown et al. 2019), and none have studied movements of captive-raised R. sierrae in streams. Because movements of released animals might strongly influence reintroduction success (McPhee and Silverman 2004), more information is needed to compare movements of wild and captive-raised R. sierrae in streams.

We investigated movements of wild R. sierrae during summer through early fall (mid-June through September or October), 2016-2018, in four diverse perennial and intermittent streams in the northern Sierra Nevada using capture-mark-recapture methods (CMR). We compared movements of wild and captive-raised individuals in one of the streams using both CMR and radiotelemetry (RT) from 2017–2018. Our objectives were to (1) quantify movements of R. sierrae in streams; (2) examine how movements differed by stream, year, and across the active season; and (3) examine how movements differed between wild and captive-raised frogs. We also (4) examined the movements of captive-raised R. sierrae after their release into a new stream environment. Our aim was to provide information to aid in the evaluation of reintroductions as a recovery tool for R. sierrae and inform the design of effective reintroduction plans.



FIGURE 1. Survey streams (red X) in northern California, USA, for Sierra Nevada Yellow-legged Frogs (*Rana sierrae*). We released captive-raised *R. sierrae* into the South Fork (SF) Rock Creek reaches (inset), which was comprised of three reaches (in red): main channel, SF Tributary 1, and SF Tributary 2. The range boundary of *R. sierrae* is outlined in black.

MATERIALS AND METHODS

Study sites.-We studied portions of two perennial streams, Independence Creek (length = 0.66 km; gradient = 2.2%) and Lone Rock Creek (length = 2.7km; gradient = 1.8%), and two intermittent streams, Mossy Pond Creek (length = 0.9 km; gradient = 16.2%) and South Fork (SF) Rock Creek (Fig. 1). SF Rock Creek consisted of three reaches, the headwaters of the main channel (SF Main Channel; length = 1 km; gradient = 9.1%), a connected tributary to SF Main Channel (SF Tributary 1; length = 1.2 km; gradient = 8.5%), and a connected tributary to SF Tributary 1 (SF Tributary 2; length = 0.4 km; gradient = 6.8%). Typical of Sierra Nevada streams, flows were high during spring snowmelt and decreased to baseflows during the summers. Snowpacks on 1 April were 94% of normal in 2016, 148% of normal in 2017, and 46% of normal in 2018 (http://cdec.water.ca.gov/snowapp/sweq.action).

Independence Creek flowed through a meadow and had multiple braided side channels that had a total length greater than that of the main channel. High flows from snowmelt inundated side channels and floodplain habitats, creating a mosaic of wetted habitats and connecting side channels to the main channel. The floodplain habitats were mostly dry by early summer in 2016 and 2018 and lasted through late summer during the high flow year 2017. Other streams had no floodplain habitat and little side channel habitat.

In the intermittent streams, surface water disconnected by mid-summer each year with only a few pools persisting by late August. As flows decreased in summers, each reach underwent different desiccation patterns. Most of SF Main Channel dried completely except for the upper sections of the reach, which retained low flow through a series of pools. Large sections of SF Tributary 1 dried, but several small sequences of pools remained connected with low flow. SF Tributary 2 dried by late summer with most water remaining in only three disconnected pools. Lastly, Mossy Pond Creek dried by early to mid-summer, with most water remaining in two disconnected pools and a small sequence of pools and chutes just above the confluence with a lake.

Data collection.—We conducted visual-encounter surveys (Heyer et al. 1994) approximately monthly from mid-June into September or October. Each site visit usually consisted of two passes of the study reach over a period that was usually four consecutive days. During each survey, at least two surveyors slowly walked the stream reach, while searching all wetted areas for all life stages of *R. sierrae*. To maximize detections, we did not survey prior to 0930 or during inclement weather. To minimize detection bias based on air and water temperatures, we typically surveyed reaches in alternating directions on consecutive surveys.

We captured frogs by hand or with a hand-net, identified, measured (snout-urostyle length; SUL), weighed, determined sex, marked, and released individuals back in their original capture location. We determined sex by the presence of nuptial pads. We inserted 12-mm PIT (Passive Integrated Transponder) tags (Avid Identification Improved Systems Inc., Norco, California, USA; Donnelly et al. 1994) into frogs > 45 mm SUL. We recorded frog locations with handheld global positioning system (GPS) devices and improved precision with waypoint averaging. We excluded from movement analyses any frogs only captured once within a given year and frogs that we could not identify by PIT tags.

We released captive-raised frogs in 2017 and 2018 into each of the SF Rock Creek study reaches (Brown et al. 2020). These frogs originated from tadpoles we collected from the SF Rock Creek drainage in 2016. We transported the tadpoles to the San Francisco Zoo where they were reared to adults. The San Francisco zoo kept both tadpoles and frogs in large volumes of water in glass enclosures that included hiding and basking spots. Tadpoles consumed spirulina-based fish foods, and frogs ate a variety of live, domestic invertebrates. The San Francisco Zoo staff minimized handling of frogs to help maintain innate anti-predation behaviors.

To increase their chances of survival, all frogs released in 2017 and two-thirds of the frogs released in 2018 were exposed to the amphibian chytrid fungus (Batrachochytrium dendrobatidis, Bd) and cleared with the antifungal drug, itraconazole, prior to release (Garner et al. 2008; Jones et al. 2012; Brown et al. 2020). Exposed frogs had three negative Bd tests before release (standard Bd DNA extraction and quantitative polymerase chain reaction methods; Boyle et al. 2004; Kriger et al. 2006; Joseph and Knapp 2018). Prevalence and loads of *Bd* on the captive-raised frogs were very low after their release in 2018, with only three frogs testing positive and with a maximum Bd load of 427 ITS1 copies per swab (Brown et al. 2020). Based on 3 y of CMR data at two reintroduction sites of the closely related Southern Mountain Yellow-legged Frog (R. muscosa), Bd-exposed frogs had slightly higher survival than unexposed control frogs (Thomas Smith and Roland Knapp, unpubl. data).

We chose release pools where wild frogs had been found and that had water in October 2016 to increase the chances that frogs would not have to search for water. In 2017, we released 22 frogs (13 males, nine females) into two pools in each of the SF tributaries. In 2018, we released 60 frogs (25 males, 35 females) into three pools in SF Main Channel, three pools in SF Tributary 1, and two pools in SF Tributary 2. Frogs released in 2018 were 1 y older than those released in 2017. Frogs averaged 50.9 ± 1.6 (standard error) mm SUL (range, 40.8-67.1 mm) in 2017 and 54.6 ± 0.9 mm SUL (range, 39.6-68.3 mm) in 2018. In both years, we divided the frogs among release sites such that sizes and sexes were distributed as evenly as possible (Brown et al. 2020).

We put waist-belt transmitters on a subset of frogs, specifically 11 frogs in 2017 (three wild, eight captiveraised) and 24 frogs in 2018 (11 wild, 13 captiveraised). We assigned transmitters to frogs distributing sexes as evenly as possible among release pools in each reach (five males and six females in 2017, 11 males and 13 females in 2018). We installed Holohil model BD-2 transmitters (0.75-1.9 g; Holohil Systems Ltd., Carp, Ontario, Canada) using aluminum beaded belts (Rathbun and Murphey 1996). Only frogs > 55 mm SUL received transmitters and packages did not exceed 10% of the body mass of the frogs (Hever et al. 1994). We replaced transmitters as needed before batteries expired (6-13 weeks depending on model weight). We tracked frogs approximately every two weeks from 18 July to 23 September 2017 and from 4 July to 2 November 2018. We located every frog at least once during a site visit, and more if time allowed. We captured and visually inspected frogs every two weeks to ensure proper belt fit and assess overall health. We removed transmitters at the end of each field season.

Analysis.—For both the CMR and RT data, we calculated stream distances between frog locations using a geographic information system (GIS; ArcGIS Desktop: Release 10.5. 2011, Esri, Redlands, California, USA). Because frogs rarely moved away from the stream channel, we analyzed distances along the stream channel rather than straight-line distances between frog locations. At Independence Creek, we also calculated movements among floodplain habitat, side channels, and main channel as straight-line distances when consecutive locations indicated that frogs likely moved laterally through floodplains.

For both the CMR and RT data, we calculated four movement response metrics for each frog: distance traveled between captures, movement rate, maximum displacement, and maximum movement. Distance traveled between captures was simply the distance moved between two sightings. Movement rate was the distance moved divided by the number of days between consecutive locations. Maximum displacement was the difference between the most distant upstream and downstream locations. Maximum movement was the greatest movement observed between consecutive site visits. Because we did not capture all frogs every visit, we standardized this metric by the number of site visits between captures; for example, the maximum distance for a frog captured in the first and recaptured in the fourth (last) CMR site visit would be divided by three. For these metrics, we only calculated movements within a year and not across years to focus on intra-annual movements.

We first used descriptive statistics with the metric, distance traveled between captures, to quantify magnitudes of movements. We calculated distances traveled within a site visit (about 1-4 consecutive survey or tracking days), between consecutive site visits (approximately 30 d for CMR, 14 d for RT), and over multiple site visits (every about 60 and \geq 90 d for CMR). We then used Linear Mixed-effects Models for movement rate, and Linear Models for maximum displacement and maximum movement using Maximum Likelihood Estimation to evaluate whether movements differed by stream reach (Site), Perenniality, Stream Stage (measured with 15-min loggers installed near the downstream end of each reach), Year, day of year from 1 January (referred to as Date), Sex, Length (frog size, mm SUL), Mass (g), and Origin (wild or captiveraised). To account for repeated measures of the same frog in the Linear Mixed-effects Models, we included frog ID (PIT number) as a random effect.

We used descriptive statistics to determine the best functional parametric form for each response and predictor variable. Based on visual examination of residual plots, we log-transformed the response variables (movement rate, maximum displacement, maximum movement) by the natural log to meet the assumptions of normality. No predictor variables required transformation. We standardized and rescaled all continuous predictor variables to have a mean of zero and a standard deviation of one.

We used Akaike's Information Criterion corrected for small sample size (AICc) to select among models with correlated predictor variables using $\Delta AICc < 2$ as the criterion (Burnham and Anderson 2002). Based on the model outputs, we selected frog Length over Mass, Date over Stream Stage, and Site over Perenniality. Because we were interested in the effects of all selected predictor variables, we evaluated the relative importance of models from all possible subsets of variables using We used Akaike weights (wi) to compare AICc. models and calculate model-averaged coefficients and 95% confidence intervals across models in the top 95% cumulative weight. We report back-transformed estimates. Finally, for movement rate models, we report movement rates as movements per month (30 d) to reflect our survey design. We conducted all analyses using the MuMIn, lme4, and AICcmodavg packages in R software (R Core Team 2013).

We examined site fidelity using the CMR data across 1 y for wild and captive-raised frogs recaptured in at least two consecutive years, and across 2 y for frogs captured in 2016 and recaptured in 2018. Because we may not have recaptured an individual at the same time each year, we used the two locations with the smallest distance difference between them for comparison, if we recaptured an individual multiple times in a year. This method yields a maximum estimate of site fidelity. Although likely an overestimate, this standardized metric is useful for comparisons among sites and between wild and captive-raised frogs. For each analysis, we compared movements between wild and captive-raised frogs. Finally, at SF Rock Creek, with the CMR and RT data, we examined the behavior of captive-raised frogs by calculating the number of days they remained in their release pools before moving and the farthest distance they traveled away from their original release pools.

RESULTS

We analyzed the movements of 203 frogs via CMR, comprising 154 wild and 49 captive-raised animals (Appendix Table). Of these, 152 were captured in just 1 y (106 wild, 46 captive-raised), 40 were captured in 2 y (37 wild, 3 captive-raised), and 11 were captured in 3 y (all wild). This yielded 524 frog locations across 2016–2018 (394 from wild frogs, 130 from captive-raised frogs). Telemetry yielded 317 locations with most frogs tracked within years. Nine of the 14 (64.3%) wild frogs and 12 of the 21 (57.1%) captive-raised frogs outfitted with radio-transmitters survived and carried



FIGURE 2. Frequency distribution of movement distances of wild and captive-raised Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) based on (A) capture-mark-recapture (CMR; n = 203 frogs) from 2016–2018 at Independence Creek, Lone Rock Creek, Mossy Pond Creek, South Fork (SF) Rock Creek Main Channel, SF Tributary 1, and SF Tributary 2, California, USA, and (B) radio-telemetry (RT; n = 32 frogs) from 2017–2018 at the three SF Rock Creek reaches. One site visit for CMR was approximately every 30 d; one tracking period for RT was approximately every 14 d.

their transmitters to the end of each tracking year. We excluded three captive-raised frogs from the analysis because in the visit following release, we tracked them to a predation event, discovered them dead, or suspected they may have died (i.e., the signal came from a persistently stationary hidden transmitter).

We found almost all frogs within 1 m of water. During a period of very high flows in 2017 at Independence Creek, we were unable to survey most of the main channel due to the high flows. In that year, 77% of sightings were in side channels, and the remainder were in or near water in floodplains; wetted floodplain habitat was not present in 2016 and 2018. At SF, the only frog that was not tracked to a stream channel was found 5 m from a channel following light rain in 2018; this frog was hidden in wet woody debris near several centimeters of water and was seen back in the stream channel 17 d later.

Capture-mark-recapture at all sites.—Wild frogs varied in their movements, with some frogs moving little, others making an occasional longer movement, and a few moving longer distances up and down the streams repeatedly (Fig. 2). Between consecutive days, the average distance wild frogs moved was 10.5 ± 2.3 m (range, 0–197.4 m), and the median distance was 3

m (interquartile range [IQR], 0-9.8 m; Fig. 2). Between consecutive site visits, the average distance wild frogs moved was 51.3 ± 8.4 m (range, 0–1,263.7 m), and the median distance was 12.7 m (IQR, 4.3-34.2 m). Among three or more site visits, the average distance wild frogs moved was 74.3 ± 13.2 m (range, 0.1–475.7 m), and the median distance was 34.8 m (IQR, 8.4-102.2 m). The largest movement a wild frog made was 197.4 m over 2 d within a site visit, 1,263.7 m over 29 d between consecutive site visits, and 475.7 m over 56 d among three or more site visits. Captive-raised frogs moved less than wild frogs between site visits but showed a similar pattern of longer movements at longer intervals (Appendix Table). Between consecutive days, the average distance captiveraised frogs moved was 6.9 ± 2.0 m (range, 0–90.7 m), and the median distance was 0.9 m (IQR, 0-7.6 m). Between consecutive site visits, the average distance captive-raised frogs moved was 16.5 ± 3.6 m (range, 0–128.2 m), and the median distance was 6.3 m (IQR, 0.6-17.6 m). Among three or more site visits, the average distance captive-raised frogs moved was 46.0 ± 29.4 m (range, 0.1-346.2 m), and the median distance was 1.8 m (IOR, 0.6–17.2 m). The largest movement a captive-raised frog made was 90.7 m over 3 d within a site visits, 128.2 m over 22 d between consecutive site visits, and 346.2 m over 53 d among three or more site visits.

TABLE 1. Mixed-effects models describing movement rate (m/d), and linear models describing maximum displacement (m) and maximum movement (m/site visit) of Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) in northern California, USA, study reaches based on capture-mark-recapture (CMR) from 2016–2018 and radio-telemetry (RT) from 2017–2018. We fitted models with Maximum Likelihood Estimation. Acronyms are AICc = Akaike Information Criterion corrected for small sample sizes and w_i = Akaike weight. Variables are defined in Materials and Methods.

	CMR Models	AICc	ΔAICc	<i>w</i> _i	RT Models	AICc	ΔAICc	W _i
Movement Rate	Origin + Site + Date	2103.1	0	0.41	Origin + Year + Date	1263.8	0	0.40
	Origin + Site + Date + Length	2104.5	1.4	0.21	Origin + Year + Date + Sex	1265.8	2.0	0.15
					Origin + Year + Date + Length	1265.9	2.0	0.14
Max Displacement		11/0 1	0	0.22		01.5	0	0.52
	Origin + Site	1160.1	0	0.32	Origin + Site	81.5	0	0.53
	Site + Length	1161.7	1.5	0.15				
	Origin + Site + Length	1161.8	1.7	0.14				
	Site	1162.1	1.9	0.12				
Max Movement	Origin + Site	886.3	0	0.23	Origin + Site + Length	75.3	0	0.33
	Site + Length	886.4	0.1	0.21	Origin + Site	75.7	0.4	0.27
	Site	886.6	0.3	0.20				
	Origin + Site + Length	887.7	1.4	0.12				

Nine movement rate models comprised 95% of the Akaike weights, though the top ranked model had almost half the weight ($w_i = 0.41$; Table 1). Site and Date appeared in all nine top models, and Year appeared only in two of the nine models each with $w_i \leq 0.05$. Estimated movement rates of captive-raised frogs were approximately half those of wild frogs, and movement rates varied by site (Table 2). For example, movement rates were lower at Lone Rock Creek than Independence Creek and lower at the two SF tributaries than SF Main Channel and Mossy Pond Creek (Fig. 3). There was little evidence that high versus low water years (defined for California as 1 October to 30 September) affected movements; models with Year had little support. Movement rates of frogs decreased from June to October by an estimated multiplicative factor of 0.60 per month (95% CI = 0.51–0.71).

Ten and 11 models comprised 95% of the Akaike weights for maximum displacement and maximum movement, respectively. Site was in all models, and Origin was in half. The top ranked model contained these predictors for both response variables (maximum displacement $w_i = 0.32$, maximum movement $w_i = 0.23$). Estimated maximum displacement and maximum movement of captive-raised frogs were about half those of wild frogs (Table 2). With the exception of SF Tributary 2, which had the smallest maximum displacement and movement, there was little evidence that maximum displacement and maximum movement varied among the remaining sites, years, sex, or size (Table 2; Fig. 4).

Radio-telemetry at South Fork Rock Creek.— Movement distances of radio-tracked wild frogs at SF Rock Creek were generally similar to those detected by CMR (Appendix Table). Between consecutive days, the average distance wild frogs moved was 15.1 ± 2.7 m (range, 0-100 m), and the median distance was 8.2 m (IQR, 3.3-21.7 m; Fig. 2). Between consecutive site visits, the average distance wild frogs moved was 21.4 \pm 4.9 m (range, 0–207.7 m), and the median distance was 8.3 m (IQR, 2.3-25.3 m). The largest movement a wild frog made was 44.3 m over 1 d within a site visits and 207.7 m over 13 d between consecutive site visits. Similar to the CMR data, radio-tracked captiveraised frogs moved less than wild frogs. Between consecutive days, the average distance captive-raised frogs moved was 4.7 ± 0.8 m (range, 0–52.4 m), and the median distance was 0.9 m (IQR, 0-6.6 m). Between consecutive site visits, the average distance captiveraised frogs moved was 7.4 ± 1.1 m (range, 0–79.5 m), and the median distance was 3.9 m (IQR, 0.9-8.4 m). The largest movements a captive-raised frog made were 52.4 m over 5 d within a site visit and 79.5 m over 13 d between consecutive site visits.

Using RT data, 11 movement rate models comprised 95% of the Akaike weights (Table 1). The top ranked model had a weight of 0.40. Origin, Year, and Date were in all the parsimonious models. Estimated movement rates of captive-raised frogs were approximately onethird those of wild frogs (Table 2). Movement rates differed little among the SF Rock Creek sites. Estimated movement rates in 2018 were more than double those of 2017, and movement rates decreased from July to

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TABLE 2. Model-averaged predictors of movement rate (m/d), maximum displacement (m), and maximum movement (m/site visit) of Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) in northern California, USA, study reaches based on capture-mark-recapture (CMR) from 2016–2018 and radio-telemetry (RT) from 2017–2018. Coefficients (β) and 95% confidence intervals (LCI = lower confidence interval) are averaged across models in the top 95% of cumulative weight. Coefficients for Date has been adjusted to reflect approximately monthly (about 30 d) changes in movement rate. All estimates are back-transformed from natural logged values. Italicized text indicates the null value (1) is not included in the CI.

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	CMR Predictors	β	LCI	UCI	RT Predictors	β	LCI	UCI
Movement Rate	Intercept (Wild; Independence Creek; 2016; Female)	1.23	0.77	1.98	Intercept (Wild; SF Main; 2017; Female)	0.62	0.30	1.29
	Captive-raised frogs	0.54	0.32	0.92	Captive-raised frogs	0.37	0.24	0.59
	Lone Rock Creek	0.52	0.24	1.13	SF Tributary 1	0.82	0.47	1.42
	Mossy Pond Creek	0.63	0.36	1.10	SF Tributary 2	0.72	0.40	1.29
	SF Main Channel	0.69	0.31	1.56	2018	2.17	1.27	3.70
	SF Tributary 1	0.49	0.26	0.92	Date	0.76	0.64	0.90
	SF Tributary 2	0.23	0.12	0.46	Male	0.92	0.59	1.44
	2017	0.98 0.62 1.56 Length		Length	1.00	0.97	1.04	
	2018	1.02	0.67	1.56				
	Date	0.60	0.51	0.71				
	Male	0.90	0.64	1.27				
	Unknown sex	1.15	0.15	8.70				
	Length	1.01	0.99	1.03				
	Intercept (Wild; Independence Creek; 2016; Female)	17.80	7.41	42.74	Intercept (Wild; SF Main; 2017; Female)	229.48	83.08	633.88
	Captive-raised frogs	0.46	0.19	1.09	Captive-raised frogs	0.25	0.13	0.45
	Lone Rock Creek	0.51	0.13	1.97	SF Tributary 1	0.46	0.21	1.04
nt	Mossy Pond Creek	1.23	0.48	3.18	SF Tributary 2	0.21	0.10	0.46
emei	SF Main Channel	1.72	0.42	7.01	2018	0.90	0.46	1.77
splac	SF Tributary 1	1.10	0.37	3.28	Male	0.87	0.49	1.56
(Dis	SF Tributary 2	0.19	0.06	0.61	Length	1.02	0.96	1.08
Мал	2017	0.70	0.34	1.41				
	2018	0.88	0.44	1.77				
	Male	1.05	0.61	1.81				
	Unknown sex	1.24	0.06	25.01				
	Length	1.02	0.99	1.05				
Max Movement	Intercept (Wild; Independence Creek; 2016; Female)	24.33	8.67	68.30	Intercept (Wild; SF Main; 2017; Female)	105.07	45.18	244.30
	Captive-raised frogs	0.53	0.21	1.36	Captive-raised frogs	0.39	0.20	0.75
	Lone Rock Creek	0.40	0.08	1.93	SF Tributary 1	0.37	0.18	0.76
	Mossy Pond Creek	0.72	0.24	2.15	SF Tributary 2	0.22	0.12	0.44
	SF Main Channel	1.34	1.34 0.28 6.47 2018		2018	0.90	0.48	1.68
	SF Tributary 1	0.99	0.29	3.39	Male	1.22	0.58	2.55
	SF Tributary 2	0.14	0.04	0.54	Length	1.05	0.99	1.12
	2017	0.95	0.47	1.92				
	2018	1.21	0.61	2.39				
	Male	0.87	0.51	1.49				
	Unknown sex	1.40	0.09	21.15				

1.05

1.02

Length

0.99



FIGURE 3. Model-averaged relationships across models in the top 95% of cumulative weight with 95% confidence intervals (shading) between (A) movement rate (lines) and Origin, Site, and Date of wild and captive-raised Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) based on capture-mark-recapture (CMR) from 2016–2018 in northern California, USA, at Independence Creek, Lone Rock Creek, Mossy Pond Creek, South Fork (SF) Rock Creek Main Channel, SF Tributary 1, and SF Tributary 2, and between (B) movement rate and Origin, Year, and Date based on radio-telemetry (RT) of wild and captive-raised frogs at all SF Rock Creek reaches in 2017–2018. Movement rate was distance/number of days between consecutive locations. For CMR, we show movement rates of females in 2018; results for males and the other years were similar. For RT, we show movement rates of females at SF Main Channel; results for males and at the other SF sites were similar. Abbreviations are P = Perennial and I = Intermittent.

October by an estimated multiplicative factor of 0.76 per month (95% CI = 0.64–0.90; Fig. 3).

Six models for maximum displacement and eight models for maximum movement comprised 95% of the Akaike weights. The top ranked model contained Origin and Site for both response variables (Table 1; maximum displacement $w_i = 0.53$, maximum movement $w_i = 0.33$). Estimated maximum displacement of captive-raised frogs was one-fourth those of wild frogs, and estimated maximum movement was more than one-third those of wild frogs (Table 2). Estimated maximum displacement and maximum movement were greatest along SF Main Channel, followed by SF Tributary 1, then SF Tributary 2 (Fig. 4).

Site fidelity of wild and captive-raised frogs.—We examined annual site fidelity between consecutive years for 52 wild and five captive-raised frogs (released in 2017 and recaptured in 2018) for 76 distance comparisons, and we examined 2-y site fidelity between 2016 and

2018 for 38 wild frogs (38 2-y distance comparisons). We recaptured 61% of the wild frogs and 40% of the captive-raised frogs within 10 m of their previous summer locations, and these spatially consistent recaptures occurred more often at Mossy Pond Creek and SF Rock Creek than the other sites. Of the 38 wild frogs that we captured in 2016 and again in 2018, we found 58% in 2018 within 10 m of their 2016 locations.

Behavior of captive-raised frogs after release.—Of the 82 frogs released into the SF Rock Creek reaches, we recaptured 52 frogs at least once. Combining both release years, 14 frogs were last seen in their release pools prior to 6 August, and we did not know if these frogs eventually left. We recaptured another 24 frogs within 25 m of their original release pools (Fig. 5). In 2017, based on CMR, the average distance captiveraised frogs moved from release sites was 10.2 ± 4.3 m (range, 0–100 m), and the median distance was 0 m (IQR, 0–4.3 m). In 2018, the average distance captive-



FIGURE 4. Model-averaged relationships across models in the top 95% of cumulative weight with 95% confidence intervals (error bars) between (A) maximum displacement (points) and Origin and Site of wild and captive-raised Sierra Nevada Yellow-legged Frogs (Rana sierrae) based on capture-mark-recapture (CMR) from 2016-2018 in northern California, USA, at Independence Creek, Lone Rock Creek, Mossy Pond Creek, South Fork (SF) Rock Creek Main Channel, SF Tributary 1, and SF Tributary 2, and between (B) maximum displacement and Origin and Site based on radio-telemetry (RT) of wild and captive-raised frogs at the SF Rock Creek reaches in 2017-2018. Maximum displacement was the difference between the most distant upstream and downstream locations. We show maximum displacements of females in 2018 for both CMR and RT; results for males and the other years were similar. Plots of maximum movements per site visit across sites for CMR and RT (not shown) are similar to this maximum displacement plot. Abbreviations are P = Perennial and I = Intermittent.

raised frogs moved from release sites was 18.5 ± 4.3 m (range, 0–346.2 m), and the median distance was 1.4 m (IQR, 0–11.9 m). The farthest distance we recaptured a captive-raised frog from its release pool was 100 m in 2017 and 346.2 m in 2018, in SF Tributary 1 and SF Tributary 2, respectively.

We successfully radio-tracked 13 of the 18 captiveraised frogs until the end of each tracking year. Eight of 13 remained in their release pools for at least a month. Frogs in SF Tributary 1 exited their pools more quickly relative to the other two SF reaches (Fig. 5). Only one captive-raised frog remained in its release pool for the duration of the tracking (SF Tributary 2 in 2018), two individuals left, but returned by the last tracking day, and 10 moved out of their release pools and settled nearby. In 2017, the average distance radio-tracked captive-raised frogs moved from release pools was 7.9 \pm 1.7 m (range, 0–40.5 m), and the median distance was 1.8 m (IQR, 0–16.9 m). In 2018, the average distance was 9.5 \pm 1.4 m (range, 0–124.6 m), and the median was 4.4 m (IQR, 0–11.7 m). Over the course of both tracking years, all but one frog (92%) remained within 50 m of their release pools, and the latter moved 124.6 m away (Fig. 5).

DISCUSSION

Understanding the movement ecology of a species can aid in the evaluation and design of recovery actions such as reintroductions for at-risk and endangered species. Our results indicate that movement patterns of endangered R. sierrae were generally site-specific and varied across the active season within diverse streams in its northern range. Wild frogs typically moved short distances (e.g., < 10 m) but were capable of making large movements as shown by one frog that moved 197 m over 2 d. This pattern of both large and small movements was similar to results from other studies. Using CMR in streams, Brown et al. (2019) reported short movements (median = 13.1 m) over 4-d periods, with greater movements by a few frogs (e.g., 207 m over about 60 d). Radio-tracked frogs from that study generally moved longer distances (average = 122 m over about 14 d) than our RT wild frogs (average < 25 m). Using CMR in a lake system, Pope and Matthews (2001) reported that 17% of PIT-tagged frogs moved between lakes that were a minimum of 66 m apart and documented one individual that moved about 600 m along a stream. Maximum distances were relatively high and similar among the three studies (range, about 840-1,264 m).

Rana sierrae is commonly cited as rarely being found > 1 m from water (Mullally and Cunningham 1956), although studies have identified overland movements (Matthews and Pope 1999; Pope and Matthews 2001; Brown et al. 2019). Our findings were consistent with both these observations. Even when frogs were away from the main channel, they were always in the water or near the edge of the water. We tracked only one frog at SF Rock Creek that was not in the stream channel, but we located it 5 m away in standing water formed by recent rain. We detected movements between the SF Rock Creek tributaries when the creek was partially dry, but whether frogs used dry stream channel, moved over land, or moved during rain is not known. In SF Main Channel, we tracked two frogs that may have moved over dry channel during one of the infrequent rains at our site. Some amphibians make large movements during rains (Daugherty and Sheldon 1982; Todd and Winne 2006; Keung 2015).

We expected to see differences in movements between high and low flows across years, across the active season, and among perennial and intermittent streams. High, fast flows might have impeded movements more in perennial streams than intermittent streams. Movements might have either increased or



FIGURE 5. (A) The maximum distances we observed captive-raised Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) away from their release pools in 2017 and 2018 based on capture-mark-recapture at South Fork (SF) Rock Creek, (B) the number of days 13 radio-tracked captive-raised frogs remained in their release pools before moving out, and (C) the maximum distances we observed 13 radio-tracked captive-raised frogs from their release pools in 2017 and 2018. The maximum possible number of days a frog could remain in its release pool was 67 in 2017 and 122 in 2018.

decreased from June to October in the intermittent sites as water availability decreased, because frogs could have travelled to remaining water or become restricted to perennial pools. Movement rates did differ among sites, but differences were not related to water permanence. For example, movement rates tended to be higher at perennial Independence Creek, where several frogs repeatedly moved relatively long distances up and down the stream, and at intermittent SF Main Channel, where frogs tended to move from the lower parts of the reach towards the perennial upstream section as the stream dried. The intermittent SF Tributary 2 was the shortest reach, had limited water availability, and had the lowest movement rates; frogs did not have to travel far to reach persistent pools where they tended to stay. The perennial Lone Rock Creek, our longest stream reach, had intermediate movement rates relative to the other streams, but also had some of the longest movements.

There was no evidence that movement rates or distances varied among high versus low water years using CMR data. In the perennial streams, frogs at Independence Creek may have been buffered from the high flows of 2017 by their shift to floodplain habitats, while few frogs were found at Lone Rock Creek during this high-water year. Intermittent streams retained water longer into the summer during 2017, but there were no sustained high

flows that might have impeded movements, and longer hydroperiods in 2017 did not facilitate greater frog movements.

The decrease in movement rates from June to October may be explained partially by limited water availability in intermittent streams, though this does not explain the decline in perennial streams. Mullally and Cunningham (1956) found that R. sierrae were widely distributed along an intermittent stream when water was plentiful but concentrated around perennial pools as streams dried. In all streams, seasonal movements related to breeding, feeding, refuge, overwintering, or other ecological requirements may also play a role (Daugherty and Sheldon 1982; Matthews and Preisler 2010). In lake populations of R. sierrae, frogs moved less in August than in September, when most frogs were migrating to different water bodies (Matthews and Pope 1999; Pope and Matthews 2001; Matthews and Preisler 2010).

We found evidence of interannual site fidelity that may be related to ecological requirements during summers, similar to *R. sierrae* in lake populations (Matthews and Preisler 2010). Of frogs recaptured across years, the majority were found at least once within 10 m of their original capture locations. Site fidelity was higher among frogs in intermittent streams than in perennial streams, which may be explained by limited water availability (Mullally and Cunningham 1956).

Captive-raised frogs released in SF Rock Creek moved less than wild frogs and tended to remain in their release pools for at least several weeks rather than dispersing immediately. Similarly, reintroduced Cryptobranchus alleganiensis bishopi moved relatively little after release prior to settling in the stream (Bodinof et al. 2012). These results suggest that immediately after release, animals familiarize themselves with their new environment. Interestingly, the captive-raised frogs released into SF Tributary 1 left their pools more quickly relative to released frogs in the other two SF reaches. This difference may be attributed to greater water connectivity at SF Tributary 1 versus the isolated pools found in the other SF reaches. In intermittent streams, flow connectivity may influence the amount and distances released frogs move within a system. Further, reintroducing animals to stable, high quality habitats, such as persistent pools, may allow acclimation to new locations and decrease the likelihood of wandering through unfamiliar environments, thus increasing survival rates (Griffith et al. 1989; Germano and Bishop 2009).

Captive-raised frogs released in 2018 moved farther than those in 2017, and our general impressions from the field were that they were harder to catch. Frogs released in 2018 were 1 y older than those in 2017, which may have influenced their movements and behavior. Another possibility is that the increased movements of captiveraised frogs in 2018 were a result of interactions with other conspecifics, including wild frogs and captiveraised frogs released in 2017. Such was the case for Leiopelma pakeka released in the second year, and researchers suggested that this movement behavior was possibly to avoid sites already occupied by frogs released in the first year (Bell et al. 2004). Further research on frog behavior, competition, and other interactions that may affect the movements of reintroduced animals are warranted, particularly for intermittent streams where aquatic habitats are less available (Dodd and Seigel 1991; Armstrong and Seddon 2008).

Our study has implications for whether reintroductions are an appropriate recovery tool for R. sierrae in streams and for designing a reintroduction program. First, captive-raised frogs initially remained near release sites for at least a few weeks, making small movements near their release pools rather than immediately leaving. This suggests that if frogs can be released into high quality habitats, they will likely remain. Second, several captive-raised frogs released in 2017 moved to new areas of the streams in 2018, suggesting that released frogs can move away from release pools should a need arise. Third, the long distances moved by some frogs suggest that released animals may be able to adjust to changing conditions such as stream desiccation. Our work suggests that conservation and reintroduction planners consider typical movement distances relative to available habitat, including seasonal differences in water availability.

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APPENDIX

APPENDIX TABLE. Summary of capture-mark-recapture (CMR) and radio-telemetry (RT) movement rates (m/d), maximum displacements (m), and maximum movements (m/site visit) for wild (W) and captive-raised (CR) Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) in northern California at South Fork (SF) Rock Creek Main Channel, SF Tributary 1, and SF Tributary 2, and for wild frogs from CMR at Independence Creek (Ind), Lone Rock Creek (LR), and Mossy Pond Creek (MP). CMR results are from 2016–2018; RT results are from 2017–2018. Movement rate was distance/# of days between consecutive locations. Maximum displacement was the difference between the most distant upstream and downstream frog locations. Maximum movement was the single largest observed movement between site visits (approximately every 30 d for CMR; approximately every 14 d for RT). Abbreviations are IQR = interquartile range and SE = standard error.

				Moveme	nt Rate (1	m/d)	Maximum Displacement (m)			Maximum Movement (m/site visit)			
				Median	Mean	Max	Median	Mean	Max	Median	Mean	Max	
Site	Method	Origin	n	(IQR)	(SE)		(IQR)	(SE)		(IQR)	(SE)		
Ind	CMR	W	13	2.2 (0.1–7.5)	5.3 (1.0)	51.4	24.0 (7.4–77.3)	60.3 (16.6)	296.1	40.3 (13.8–99.4)	69.0 (21.8)	296.1	
LR	CMR	W	13	0.4 (0–3.5)	6.8 (2.7)	78.3	6.0 (1.4–97.0)	166.8 (85.4)	1,263.7	19.0 (0.7–196.7)	215.4 (128.5)	1,263.7	
МР	CMR	W	89	0.5 (0.3–1.5)	2.2 (0.4)	27.1	19.6 (9.0–76.9)	69.7 (11.4)	669.8	15.9 (7.7–53.8)	63.4 (11.5)	669.8	
		W	5	1.3 (0.3–4.1)	3.5 (1.5)	22.5	30.0 (14.6–129.2)	83.7 (37.5)	267.5	59.9 (10.8–99.8)	82.7 (41.1)	267.5	
Main	CMR	CR	13	0.4 (0-3.1)	2.4 (0.7)	18.7	14.7 (12.1–25.2)	27.1 (9.0)	128.2	22.7 (18.5–50.2)	46.3 (21.5)	128.2	
SFI		W	3	1.0 (0.3–3.5)	4.4 (1.5)	40.7	264.3 (162.3–267.0)	198.1 (68.9)	269.6	205.6 (116.9–206.7)	147.2 (59.5)	207.7	
	RT	CR	4	0.8 (0–4.2)	3.2 (0.7)	18.3	58.2 (46.8–82.3)	70.9 (24.8)	141.5	49.3 (40.2–59.2)	50.1 (11.8)	79.5	
		W	20	0.6 (0–1.8)	2.2 (0.6)	34.0	30.7 (6.0–96.7)	68.9 (16.8)	373.4	35.2 (13.1–64.1)	42.2 (7.3)	124.5	
lb. 1	CMR	CR	18	0.8 (0–2.6)	3.2 (1.1)	30.2	16.7 (6.5–73.9)	43.3 (12.6)	205.4	21.4 (7.5–65.7)	37.0 (9.4)	107.6	
SF Tı		W	4	1.6 (0.3–4.9)	5.4 (1.6)	44.3	98.0 (81.8–113.0)	96.8 (13.3)	126.4	30.1 (24.2–37.7)	31.8 (6.8)	49.5	
	RT	CR	7	0.4 (0–1.2)	1.4 (0.4)	18.8	25.3 (22.4–25.8)	24.9 (1.9)	34.3	16.6 (14.6–20.6)	17.6 (1.6)	23.5	
		W	14	0.2 (0–1.6)	3.3 (2.3)	98.7	6.2 (2.4–26.8)	36.3 (14.7)	197.4	4.3 (2.3–15.7)	25.6 (12.6)	147.0	
ib. 2	CMR	CR	18	0 (0–0.3)	0.9 (0.3)	11.8	2.2 (0-6.2)	24.5 (17.3)	346.2	3.1 (0.4–6.2)	17.7 (14.2)	173.1	
SF Th		W	7	1.3 (0.3–3.7)	2.5 (0.4)	11.3	37.3 (33.8–73.1)	67.0 (23.9)	198.6	37.3 (31.3–41.6)	41.8 (9.5)	94.8	
	RT	CR	7	0.3 (0–0.7)	0.9 (0.3)	12.3	6.5 (4.8–26.8)	16.6 (6.2)	44.8	6.5 (3.8–14.4)	10.0 (3.3)	25.6	
All	CMR	W	154	0.6 (0.1–2.7)	3.3 (0.4)	98.7	19.6 (6.2–78.9)	73.2 (9.6)	1263.7	17.4 (6.7–67.9)	67.0 (10.5)	1,263.7	