*Herpetologica*, 69(2), 2013, 147–162
© 2013 by The Herpetologists' League, Inc.

# POPULATION SIZE, SURVIVAL, GROWTH, AND MOVEMENTS OF *RANA SIERRAE*

Gary M. Fellers[1,4], Patrick M. Kleeman[1], David A. W. Miller[2], Brian J. Halstead[3], and William A. Link[2]

[1]*US Geological Survey, Western Ecological Research Center, Point Reyes National Seashore, Point Reyes, CA 94956, USA*
[2]*US Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Dr., Laurel, MD 20708, USA*
[3]*US Geological Survey, Western Ecological Center, Dixon Field Station, 6924 Tremont Road, Dixon, CA 95620, USA*

Abstract: Based on 2431 captures of 757 individual frogs over a 9-yr period, we found that the population of *R. sierrae* in one meadow–stream complex in Yosemite National Park ranged from an estimated 45 to 115 adult frogs. *Rana sierrae* at our relatively low elevation site (2200 m) grew at a fast rate ($K = 0.73$–0.78), had high overwintering survival rates (44.6–95%), lived a long time (up to 16 yr), and tended to be fairly sedentary during the summer (100% minimum convex polygon annual home ranges of 139 $m^2$) but had low year-to-year site fidelity. Even though the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*, *Bd*) has been present in the population for at least 13 yr, there was no clear downward trend as might be expected from reports of *R. sierrae* population declines associated with *Bd* or from reports of widespread population decline of *R. sierrae* throughout its range.

*Key words*: Growth; Movement; Population size; *Rana sierrae*; Sierra Nevada; Sierra Nevada Yellow-legged Frog; Survival

*Rana sierrae* (Sierra Nevada Yellow-legged Frog) is endemic to the central and northern Sierra Nevada of California where the population extends 475 km along the crest of the mountains within an elevational range of 1370–3690 m. In the early 1900s, *R. sierrae* was an abundant frog throughout high elevations within its range. Grinnell and Storer (1924) described these frogs as the most abundant amphibian at high elevation sites in Yosemite National Park (NP). Their notes state that "hundreds of frogs" were at Young Lakes, and frogs were "very numerous" at Westfall Meadow (Charles Camp field notes, June and July 1915; on file Museum of Vertebrate Zoology, U.C. Berkeley). By 1992, *R. sierrae* had nearly disappeared from the sites surveyed by Grinnell and Storer (Drost and Fellers, 1996). More recently, Vredenburg et al. (2006) reported that *R. sierrae* had been extirpated from 92.5% of 146 historic sites throughout their range. While the cause of these declines is still under investigation, it is likely to be the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*, *Bd*; Fellers et al., 2001; Briggs et al., 2010), nonnative trout (Knapp and Matthews, 2000; Knapp et al., 2007), pesticide exposure (Sparling et al., 2001; Sparling and Fellers, 2007, 2009), or a combination of factors (Sodhi et al., 2008).

The first significant ecological study of *R. sierrae* was conducted by Zweifel (1955) who looked at *R. boylii*, *R. muscosa*, and *R. sierrae* in the United States as well as several related species in Mexico. Zweifel provided detailed information on all life stages including their natural history and relationship to sympatric and closely allopatric species in the *R. boylii* complex. More recent studies have examined *R. sierrae* movement and habitat use (Matthews and Pope, 1999), movement and seasonal distribution (Pope and Matthews, 2001), and site fidelity (Matthews and Preisler, 2010) at a high-elevation site (Dusy Basin) near the southern end of the range. Matthews and Miaud (2007) used skeletochronology to look at age structure, growth, and longevity of *R. sierrae* (and one population of *R. muscosa*) throughout the range of *R. sierrae*. Most recent work has focused on the role of *Bd* in population declines in the Sierra Nevada (Vredenburg et al., 2010).

Some populations of *R. sierrae* have persisted in the presence of factors typically associated with amphibian extirpations. Field experiments conducted at our study site in

[4] Correspondence: e-mail, gary_fellers@usgs.gov

Summit Meadow, Yosemite NP in 2001 and 2002 demonstrated that pesticides were having a deleterious effect on survival and development of *Pseudacris regilla* (Pacific Chorus Frog; Cowman, 2005). Furthermore, *Bd* has been present at this site since at least 1998 (Fellers et al., 2001) and has been documented there each year we have sampled for it: 2001, 2004, 2005, 2006, 2007, and 2011 (Fellers et al., 2011; D. E. Green, personal observation).

All ecological studies of *R. sierrae* in the last 2 decades have used populations at high elevations (3250–3650 m) at the southernmost portion of the range and in alpine lakes and ponds which are rocky and relatively barren (e.g., Matthews and Pope, 1999; Pope and Matthews, 2001; Matthews and Preisler, 2010). Our work was carried out in a wet meadow–stream system with extensive wetland vegetation located in a lower portion of their elevational range (2220 m).

In this paper we present a detailed summary of the population dynamics of what has been a relatively stable population of *R. sierra*. We believe the work provides a benchmark for comparison with other populations and important insights into the basic population ecology of this species. Our study was designed to estimate the size of the adult population of *R. sierrae* within a meadow–stream complex in Yosemite NP, examine growth and survival rates, and evaluate movements of individual adult frogs. We were not specifically looking at the impact of disease or pesticides, but companion studies simultaneously conducted at our study area may provide insight into the complex environmental factors that could be affecting the local *R. sierrae* population.

## Materials and Methods

### *Study Area and Species*

Our study site was Summit Meadow, a 1.5-km long, fishless, meadow–stream complex (2220 m elevation) along the Glacier Point Road in Yosemite NP, California. The area adjacent to the meadow–stream complex was predominantly Lodgepole Pine (*Pinus contorta*) forest with some Red Fir (*Abies magnifica*). In the meadows and along the stream corridors the predominant vegetation was Willow (*Salix jepsonii*), Corn Lily (*Veratrum californicum*), Small Camas (*Camassia quamash*), and Broad-leaf Lupine (*Lupinus latifolius*). No nonnative plants have been identified within our study area (P. Moore, personal observation). The forest did not provide any suitable habitat for breeding or feeding because it was covered with snow in the winter and dry for most of the summer and fall. The nearest meadow complex not in our study area lies 1.5 km to the east, but we have not found *R. sierrae* in that meadow complex.

*Rana sierrae* occur throughout the meadow–stream complex. Frogs breed just as the snow melts in the late spring or early summer, often in ponds or pools that are still surrounded by snow and partially frozen over. Breeding is completed well before snow completely melts from the meadow–stream complex. We used a snow sensor at Gin Flat (Yosemite NP, 2150 m elevation, 14.9 km NW of Summit Meadow) to document when snow had completely melted for each year. During the 8 yr of our study, the first day of field work ranged from 23 to 76 d after snow was completely gone from the meadow (Table 1).

Other anurans breeding at our study site included a few *Bufo canorus* (Yosemite Toads) and large numbers of *P. regilla*. At our study site, *R. sierrae* tadpoles spend three summers as larvae, transforming at the end of the third summer when they are 2.5 yr old. Juveniles take 3.5 yr to reach sexual maturity (Zweifel, 1955; Matthews and Miaud, 2007) so frogs typically become sexually mature after 6 yr.

### *Mark–Recapture Sampling Schedule*

Fieldwork took place during the summers of 2003–2011 using a robust design sampling protocol (Pollock, 1982). From 2003–2006 we caught frogs on three consecutive days in each primary capture period, with four primary periods each summer. From 2007–2011 we caught frogs on four consecutive days per primary capture period (except for one primary period in 2009 which only had 3 capture-days), with three primary periods each summer. The mean number of days between primary capture periods within each

TABLE 1.—Dates of snowmelt at Gin Flat, Yosemite National Park (2150 m elevation), 14.9 km NW of our study site at Summit Meadow (2220 m), and of our first capture for *Rana sierrae*.

| Gin Flat snowmelt | First sampling date for year | Days after snowmelt |
|---|---|---|
| 04 June 2003 | 19 August 2003 | 76 |
| 03 May 2004 | 13 June 2004 | 41 |
| 12 June 2005 | 05 July 2005 | 23 |
| 29 May 2006 | 11 July 2006 | 43 |
| 06 May 2007 | 03 July 2007 | 58 |
| 31 May 2008 | 08 July 2008 | 38 |
| 14 May 2009 | 07 July 2009 | 54 |
| 15 June 2010 | 27 July 2010 | 42 |

year was 12.2 ± 4.2 d. The first day of fieldwork for each year is shown in Table 1.

### *Survey Techniques*

During each survey, we attempted to capture every frog. We located frogs during diurnal searches of the stream and associated meadow system. We alternated where we began our daily searches within the study area to ensure that all areas were regularly searched during peak activity periods during the day. Frogs were usually sitting on the bank immediately adjacent to the water, but occasionally frogs were found up to 0.5 m away from the water or while sitting underwater or swimming. When there was not too much vegetation, we used binoculars to scan ahead for frogs that might be basking; however, about a third of the frogs were first noticed as they jumped into the water. We encouraged this behavior by gently swinging a dip net along the bank as we walked so that frogs we might have overlooked would reveal themselves by jumping.

### *Handling and Marking*

Frogs were caught with a dip net or by hand and immediately processed and released at the point of capture. Frogs <4.0 cm snout–vent length (SVL) were released without processing. Larger frogs were weighed to the nearest 0.1 g with a spring scale (Pesola AG), measured to the nearest millimeter with a wooden ruler, and tagged by inserting a passive integrated transponder (PIT) tag (Biomark, Inc.) under the dorsal skin. At the beginning of the study we used 12.5 × 2.5-mm PIT tags but in 2006 we began using smaller 9 × 2.5-mm tags. Sex was determined by examining the thumbs to see if they had conspicuous nuptial pads, as is typical of males (Zweifel, 1955). The universal transverse Mercator (UTM) coordinates were recorded for each frog on each capture using a GPS receiver (Garmin eTrex Legend HCx, Garmin Ltd.). This model uses the Wide Area Augmentation System to obtain position accuracy to within 3 m. Frogs recaptured within the same week were released immediately after recording the PIT tag number and UTMs.

In 2010 we began using a PIT tag scanner with a 0.8-m wand antenna (Agrident AEA080, Agrident Corp.). This allowed us to reach out slowly to scan a resting frog. If the frog had a PIT tag and had been captured earlier that week, its location and tag number were recorded but the frog was not captured. This reduced handling stress for the frog and increased our detection efficiency.

### *Precipitation*

We evaluated precipitation using data from a river flow gauge operated by the US Geological Survey on the Merced River, which drains the basin where our study site was located. The river gauge was 62 km WSW of the study site. We quantified annual precipitation by comparing the volume of water flowing in the Merced River for each year with the 50-yr average for years 1951–2000 (http://cdec.water.ca.gov/cgi-progs/profile?s=MRC&type=fnf). Because the majority of precipitation occurs as snow in the winter months, which span two calendar years, we defined annual precipitation as beginning on 1 September and ending on 31 August of the following year.

### *Statistical Analysis*

*Survival and population size*.—The population of *R. sierrae* in our study area was defined as the frogs that use the meadow–stream complex during at least some part of the summer months. We estimated survival and population size using a robust design estimator that allows for temporary emigration of individuals from the study site (Kendall et al., 1997; Mazerolle et al. 2007; Schmidt and

Pellet, 2009; Wagner et al., 2011). We fit models with the program MARK (White and Burnham, 1999) using a parameterization where abundance is included in the likelihood. We were interested in estimating sex-specific abundance and survival. Therefore, we did not include data for juvenile frogs. In cases where frogs were initially caught as juveniles and subsequently caught as adults, data for the individual was included beginning at their first capture as an adult.

We evaluated relative fit of different models using Akaike's information criterion (AIC; Burnham and Anderson, 2002). The models included parameters for temporary emigration probability, detection probability, survival probability, and abundance. For each of these parameter types we developed a limited set of alternative parameterizations. Comparing all combinations of all parameters would lead to an unwieldy number of alternatives, so we fit the model piece-wise. We first considered alternatives for emigration using the most general model for other parameter types. We then used the parameterization for emigration that had the lowest AIC value when considering alternative models for detection and then, in the same manner, moved to survival and then abundance.

We considered three general alternatives for temporary emigration: (1) no temporary emigration, (2) the probability an individual was present did not depend on whether it was present in the previous primary capture period (random), and (3) the probability an individual was present depended on whether it was present in the previous primary capture period (Markovian). For random and Markovian emigration we considered alternatives where parameters were constant, differed by sex, differed among primary capture periods, and differed by sex and capture period. Including temporary emigration in the model allowed us to account for variability in whether individuals were readily available for capture. We believe it was rare for individuals actually to leave the population. However, local movements may lead to periods when individuals were not available for capture in the study area.

For detection we considered alternatives where detection was constant, differed by sex, differed among primary capture periods, and differed based on behavior (i.e., the probability of capturing an individual the first time in a period differed from the probability of subsequent recapture). In addition, we considered all additive combinations of sex, time, and behavior effects.

For survival we considered models where survival was constant, varied between sexes, varied among years, and varied between seasons (summer = first to last primary session within a year; winter = last primary session in a year to the first primary session in the following year). We considered additive combinations of each as well as interactions between year and sex.

For abundance we considered models where abundance differed among years, capture sessions, and between sexes (not a 1:1 sex ratio). In addition, we included additive combinations of time and sex as well as their interaction.

We then evaluated the effect of precipitation on both estimated survival and estimated population size. For survival, we evaluated the relation between precipitation (which occurs mostly in the winter) and (1) winter survival that same winter, and (2) summer survival during the subsequent summer. For adult population size we evaluated the relationship between precipitation and population size during the subsequent summer and precipitation in each of the six prior years. This was based on the idea that tadpoles spend three summers before metamorphosis, newly metamorphosed frogs reach sexual maturity after an additional 3 yr, and years with low precipitation tend to concentrate the metamorphs and small adults close to water bodies where they might have a higher risk of predation. To do this we calculated the correlation between estimated abundance and precipitation for all lag-times between 0 and 6 yr.

*Growth.*—We fit von Bertalanffy growth curves for both male and female frogs using a hierarchical model that accounts for individual variation in growth and measurement error when estimating growth from capture–recapture data (Eaton and Link, 2011). We fit the growth model using Markov Chain Monte Carlo methods in OpenBUGS (Spiegelhalter

et al., 2011). For fitting the model we used the age at sexual maturity (6 yr post-egg stage) as the starting size for the growth curves. We were able to estimate the initial size at maturity from the model based on individuals initially caught as juveniles and subsequently caught as adults. We did not include frogs <4.0 cm because most were too small to tag and because they do not reach sexual maturity until they are ≥4.0 cm. Three primary parameters define the growth curve: starting size (s[0]), asymptotic size (a), and growth rate (K). We also estimated the standard deviation of starting size (sd[s]), measurement error (sd[e]), and a parameter ($\lambda$) related to individual variation in growth; $\lambda$ is the mean-to-variance ratio in the von Bertalanffy model (see Eaton and Link [2011] for a detailed description). All parameters except measurement error were allowed to differ between males and females.

*Frog movements*.—We examined daily movement by calculating the straight-line distance between successive captures of individuals. To avoid underestimation of movements of frogs with multiday capture intervals, we restricted the analysis to individuals that were captured on consecutive days. We looked at the effects of sex, SVL, and their interaction on daily movement distance using linear mixed models. We conducted a similar analysis for annual movement distances, where annual movement distance was defined as the distance between the last location of an individual in a given year and its subsequent location after a single winter had passed. We log-transformed daily and annual movement distances (excluding intervals over which no movement occurred) and standardized SVL to zero mean and unit standard deviation prior to analysis. Random intercepts for individual and year were included to account for multiple movements of the same individuals and temporal heterogeneity not explained by the covariates. To determine the posterior probability of each model, we performed an all-subsets regression for the fixed effects using an indicator variable on each model coefficient for the full sex × SVL interaction model (Kuo and Mallick, 1998; Royle and Dorazio, 2008). We then calculated model-averaged predictions by multiplying the estimated coefficient by the indicator variable at each iteration for selected covariate profiles. We selected priors for each model to be uninformative (model intercept and coefficients = $N[0,100]$, standard deviations = $U[0,10]$, indicator variables = $Bern[0.5]$). We ran each model on three chains of 100,000 iterations each after a burn-in of 10,000 iterations and thinned the output by a factor of three. Convergence was assessed visually with history plots and the Gelman–Rubin statistic (Gelman et al., 2004), and model fit was assessed with a Bayesian *P*-value (Kéry, 2010). No evidence for lack of convergence or model fit was observed.

We examined space use with 100% minimum convex polygon (MCP) summer home ranges for individuals captured on five or more occasions within a season. Summer home ranges were defined as the space use of individuals in July and August, when the majority of our field sampling was conducted. MCPs were used because more complex home range estimators were inappropriate given the limited number of captures of individual frogs. Effects of sex, SVL, and their interaction on MCP area were examined using linear mixed models as described above for frog movements.

MCPs could be calculated in more than 1 yr for seven individuals; for these frogs we calculated the distance between MCP centroids and also calculated home range overlap between years. We calculated overlap by dividing the area of intersection of the two annual MCPs by the area of the first MCP, resulting in the proportion of the first MCP overlapped by the second MCP.

We used R 2.12.2 (R Development Core Team, 2011) with packages adehabitat (Calenge, 2006) and gpclib (Peng et al., 2010) for analysis of frog space use. We used WinBUGS 1.4.3 (Spiegelhalter et al., 2003), called through R via the package R2WinBUGS (Sturtz et al., 2005), to fit models, estimate parameters, and predict space use for frogs with varying individual characteristics. Other statistics were calculated using Statistix (Version 7, Analytical Software, Tallahassee, FL). We used $\alpha = 0.05$ to evaluate statistical significance.

TABLE 2.—Best models (ΔAICc < 5.0) for *Rana sierrae* abundance and survival at Summit Meadow, Yosemite National Park, 2003–2011. Temporary emigration was modeled as a Markovian process with emigration probability varying among primary capture sessions. Detection differed among sessions and between sexes. Parameters in the survival (S) and abundance (N) parameterizations included year, sex, session, and season, where the year was divided into the period between the first and last session in a year and the period from last primary period in 1 yr to the first session in the following year.

| Model | AICc | ΔAICc | No. of parameters |
|---|---|---|---|
| Abundance models | | | |
| S(year + sex) N(year) | 3900.5 | 0.0 | 110 |
| S(year + sex) N(year + sex) | 3900.6 | 0.1 | 111 |
| S(year + sex) N(Session + sex) | 3905.1 | 4.6 | 133 |
| Survival models | | | |
| S(year + sex) N(session*sex) | 3953.8 | 0.0 | 163 |
| S(year + sex + season) N(session*sex) | 3955.7 | 1.9 | 164 |
| S(year + season) N(session*sex) | 3955.8 | 2.1 | 163 |

## RESULTS

### *Population Size and Survival*

From 2003–2011 we marked 757 individual frogs: 348 males, 316 females, and 93 juveniles. We had 2431 total captures and 1674 recaptures involving 513 individual frogs.

Model selection for our mark–recapture analysis supported a model where temporary emigration was Markovian and varied among primary sampling periods. The best detection model included differences among primary sampling periods and between sexes. There were multiple models for abundance with good support (ΔAICc value of <5.0; Table 2), so we used model averaging to account for this uncertainty when generating estimates (Burnham and Anderson, 2002). The top two models both included variation in abundance among years but not within years. In one of the top two models, the sex ratio differed from 1:1 and in the other it did not.

We calculated population size for each of the 9 yr of the study. The estimated number of *R. sierrae* in our study area ranged from lows of 22 males and 23 females in 2003 to 61 males and 54 females in 2007. Averaged across all years, the total population of adult *R. sierrae* was estimated at 86 frogs, with 45 males and 41 females, for an average sex ratio of 1:0.9 (male:female; Fig. 1). The estimated sex ratio ranged from 1:0.8 in 2009 to 1:1.1 in 2003.

Between the 1996–1997 and 2010–2011 water years, annual Merced River flow ranged from 51% to 190% of the 50-yr average (Table 3). The correlation between population size and precipitation was positive for lags of 0 to 2 yr, with the strongest correlation occurring for 2 yr prior (current year = 0.25, 1 yr prior = 0.21, 2 yr = 0.74, 3 yr = –0.05, 4 yr = –0.59, 5 yr = –0.21, and 6 yr = –0.44; Fig. 2).

There was strong support for annual differences in survival. Sex and seasonal differences also occurred in the top models but support for these was much weaker (Table 2). This was reflected in the parameter estimates where survival within years was nearly identical for both males and females, and for winter and summer, but varied a great deal from year to year (Table 4). To make estimates comparable between seasons and to other studies, we standardized survival estimates to be equivalent to the probability of surviving 1 yr.

Approximately 70% of both males and females survived each year. Survival between summer capture periods ranged from 50.2% for males during the summer of 2007 to 98.8% for both males and females during 2006. Winter survival, from the last capture period in one summer to the first capture period in the subsequent summer, ranged from 44.6% for males in 2007–2008 to 95.0% for both males and females during the 2006–2007 winter (Table 4).

When examining the relationship of survival to annual precipitation, the best model (ΔAICc = 0) was one where survival was a function of precipitation in the previous year. The model with no precipitation effects had a ΔAICc of 0.77 and the model for which

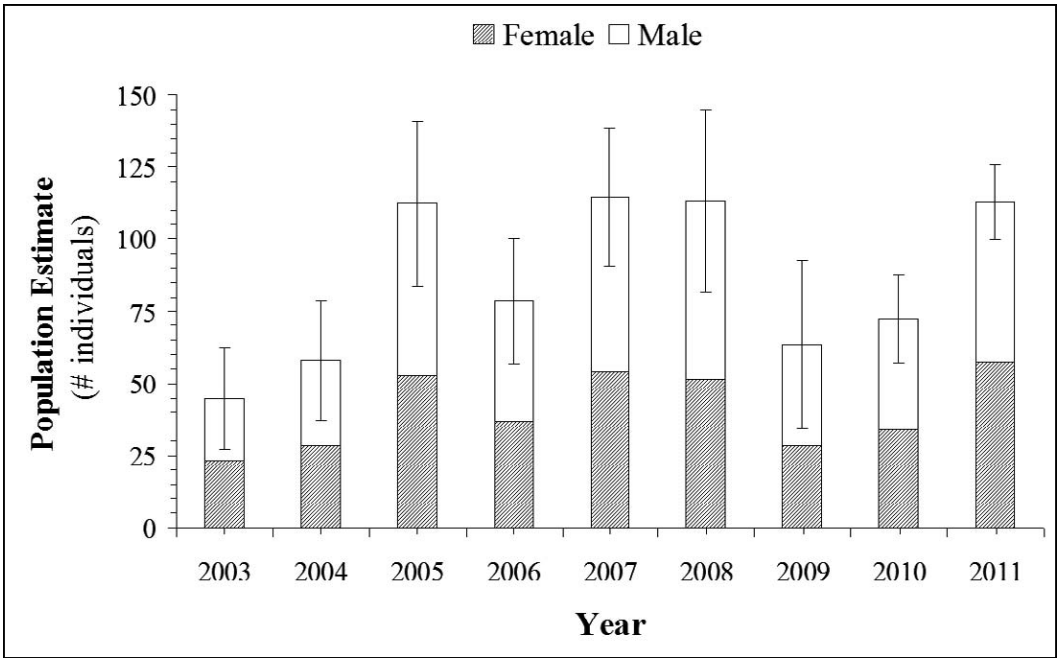


FIG. 1.—*Rana sierrae* population estimate (±SE) at Summit Meadow, Yosemite National Park, 2003–2011. Error bars are mean SE for the total population.

precipitation in the current year predicted survival had a ΔAICc of 2.88. The estimated effect on a logit-scale (±SE) for a 1 SD increase in precipitation was 0.41 with a confidence interval that included 0 (–0.07, 0.89). This was consistent with survival being, on average, 14% greater when annual precipitation was at the level we observed in the wettest year compared to the value we observed in the driest year.

TABLE 3.—Water flow in the Merced River from 1 September of the first year through 31 August of the second year. Percent flow indicates flow for that year compared to the 50-yr average from 1951–2000.

| Year | Percent flow |
|---|---|
| 1996–1997 | 172 |
| 1997–1998 | 182 |
| 1998–1999 | 89 |
| 1999–2000 | 96 |
| 2000–2001 | 51 |
| 2001–2002 | 63 |
| 2002–2003 | 80 |
| 2003–2004 | 60 |
| 2004–2005 | 166 |
| 2005–2006 | 172 |
| 2006–2007 | 41 |
| 2007–2008 | 61 |
| 2008–2009 | 82 |
| 2009–2010 | 105 |
| 2010–2011 | 190 |

In 2004, 58 adult *R. sierrae* were swabbed at Summit Meadow to evaluate the prevalence of *Bd*. Frogs that were *Bd* negative were last captured a mean of 611 d (range = 0–2562, $n = 33$) after being swabbed, while frogs with 1–20 zoospore equivalents were last seen 303 d later (0–2162, $n = 16$) and frogs with 20–200 zoospore equivalents were last captured 329 d later (0–771, $n = 9$). The mean for all *Bd*-positive frogs at last capture was 312 d (*Bd* infection status, C. Briggs, personal observation). There was no significant difference in time of survival time for the two *Bd*-positive groups of frogs ($t = 0.13$, $P = 0.898$) or when comparing *Bd*-positive and *Bd*-negative frogs ($t = 1.84$, $P = 0.071$). Hence, though *Bd*-negative *R. sierrae* adults were last captured after almost twice as many days as frogs that were *Bd* positive when first swabbed, survival time was sufficiently variable to make the difference nonsignificant in our sample.

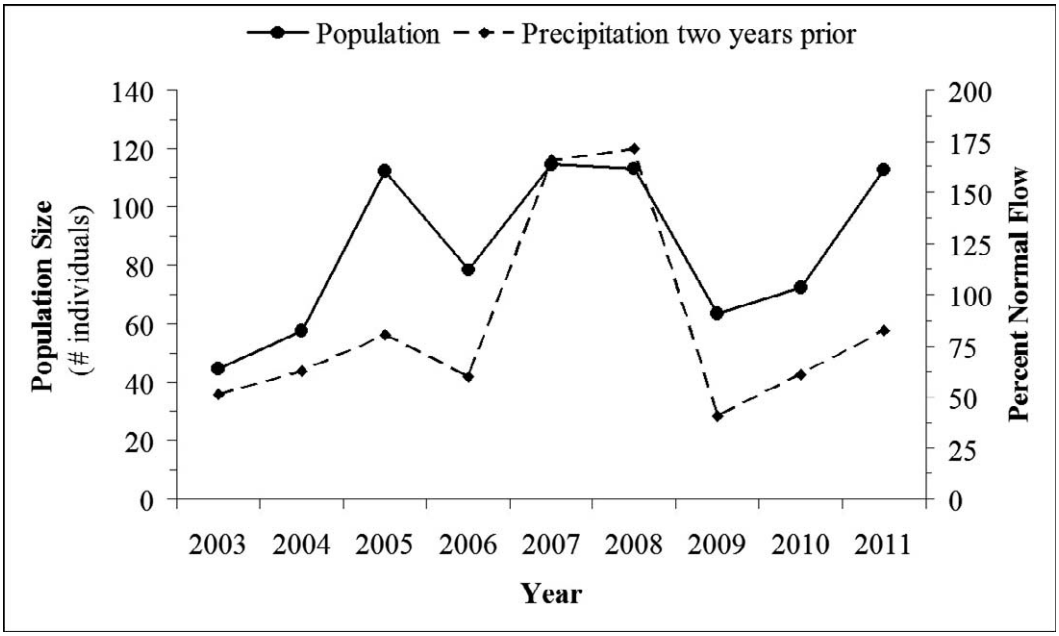


FIG. 2.—Population size and precipitation 2 yr earlier, as measured by annual flow in the Merced River, Yosemite National Park.

TABLE 4.—Summer and winter survival (±1 SE) for male and female *Rana sierra*. Summer survival is for the first year listed in the range of years and winter survival spans the two calendar-years. Survival for both seasons is standardized to the percentage of individuals surviving one year.

| Year | Summer survival | Winter survival[a] |
|---|---|---|
| Males | | |
| 2003–2004 | 87.9 ± 18.0 | 87.6 ± 12.5 |
| 2004–2005 | 70.5 ± 19.0 | 70.8 ± 10.2 |
| 2005–2006 | 59.4 ± 22.4 | 58.3 ± 6.5 |
| 2006–2007 | 98.8 ± 2.2 | 95.0 ± 8.7 |
| 2007–2008 | 50.2 ± 25.7 | 44.6 ± 6.7 |
| 2008–2009 | 74.3 ± 21.2 | 77.1 ± 10.2 |
| 2009–2010 | 54.7 ± 25.1 | 51.0 ± 9.3 |
| 2010–2011 | 65.7 ± 27.8 | 66.5 ± 17.3 |
| 2011 | 93.7 ± 16.4 | – |
| Mean | 72.8 ± 19.8 | 68.9 ± 10.2 |
| Females | | |
| 2003–2004 | 88.2 ± 17.7 | 87.7 ± 12.3 |
| 2004–2005 | 70.9 ± 18.8 | 71.2 ± 10.2 |
| 2005–2006 | 59.8 ± 22.3 | 58.7 ± 6.6 |
| 2006–2007 | 98.8 ± 2.2 | 95.0 ± 8.7 |
| 2007–2008 | 50.5 ± 25.6 | 45.1 ± 6.8 |
| 2008–2009 | 74.6 ± 21.0 | 77.4 ± 10.1 |
| 2009–2010 | 55.1 ± 25.0 | 51.5 ± 9.5 |
| 2010–2011 | 66.1 ± 27.7 | 67.0 ± 17.3 |
| 2011 | 93.8 ± 16.1 | – |
| Mean | 73.1 ± 19.6 | 69.2 ± 10.2 |

[a] (–) = not applicable.

We occasionally found *R. sierrae* subadults that had recently died or were lethargic and obviously near death. Two such subadults were collected 12 August 2010 and 1 September 2011 and sent to the USGS National Wildlife Health Center (Madison, WI); both were strongly *Bd* positive based on histological or cytological examination (D. Earl Green, personal observation).

### *Size, Growth, and Longevity*

We compared the size of male and female frogs using measurements from the last day each frog was weighed and measured during the study. Male *R. sierrae* were significantly smaller than females (Table 5) both in mean SVL ($t = 8.94$, $P < 0.001$) and mean mass ($t = 9.89$, $P < 0.001$). Because all frogs were measured well after the breeding season, which occurs right at snowmelt, female weights did not include gravid females.

We estimated the average size when frogs reached sexual maturity as 4.4 (95% Bayesian credible interval: 4.3–4.5) cm for males and 4.5 (4.4–4.7) cm for females. Both males and females approached asymptotic sizes at similar rates with females growing only slightly faster

TABLE 5.—Snout–vent length (SVL) and mass at last capture for adult *Rana sierrae* in 2011.

| | SVL (cm) | | Mass (g) | | |
|---|---|---|---|---|---|
| Sex | Mean ± SE | Range | Mean ± SE | Range | *n* |
| Male | 5.6 ± 0.04 | 4.1–7.1 | 19.8 ± 0.4 | 6.8–48.3 | 352 |
| Female | 6.3 ± 0.07 | 4.1–8.5 | 29.4 ± 0.9 | 7.5–73.5 | 323 |

than males ($K = 0.78$ [0.67–0.89] for females; $K = 0.73$ [0.60–0.86] for males; Fig. 3). Both sexes approached their asymptotic size 3–4 yr after sexual maturity with a mean maximum SVL of 6.5 (lmax = 6.4–6.7) cm for males and 7.6 (7.5–7.7) cm for females. The SD of measurement error for the above SVLs was 0.24 (0.23–0.26) cm; this includes actual variation in measurements and additional variation because we treated growth as constant throughout the year. In addition, we found significant variation among individuals in growth rates (Fig. 3). The estimated value of $\lambda$ (= individual variation in growth) was 93 (62–134) for females and 76 (49–117) for males.

When age at sexual maturity (6 yr, including the 3-yr tadpole stage) is added to the start of the growth curve, frogs reach an asymptote at about 10 yr of age. At least some *R. sierrae* survive beyond this age, as shown by the long intervals between captures in some individuals. We had 643 individual frogs that were captured in more than 1 yr. These included spans of 1 yr (318 frogs), 2 yr (179), 3 yr (80), 4 yr (35), 5 yr (19), 6 yr (8), and 7 yr (4). We used the growth curve to estimate the age at first capture and then added the time until last capture to calculate age at last capture. For frogs that were recaptured at least once, the average age at last capture was 8.4 yr for males and 8.5 yr for females. Those ages might be an underestimate for frogs that fell on the asymptotic portion of the curve because they were recorded as being 10 yr old at first capture, even though they could have been older. Nonetheless, there were 15 frogs that were estimated to be 14–16 yr old when last caught (Table 6).

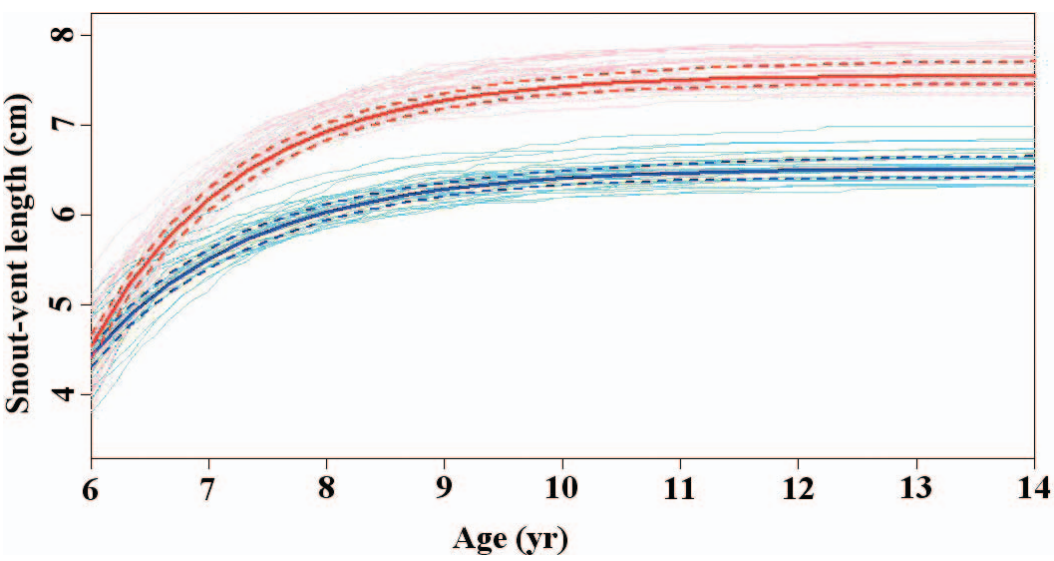


FIG. 3.—Growth in snout–vent length (SVL) from age at sexual maturity for male (blue; lower set of lines) and female (red, upper set of lines) *Rana sierrae* at Summit Meadow, 2003–2011. Because it takes 2.5 yr from egg to metamorphosis, and almost 3.5 more years to reach sexual maturity, a frog is 6 yr old at sexual maturity. Dark solid lines represent mean sizes at each age and dashed lines represent 95% credible intervals. To demonstrate estimated individual variation in growth we also plotted 30 randomly generated growth trajectories (thin light lines).

TABLE 6.—*Rana sierrae* with the longest intervals between first and last captures. Lengths (snout–vent), weights, and intervals are for the first and last capture for each individual. The estimated age at first capture assumes that it takes 2.5 yr from egg to metamorph and 3.5 subsequent years for a metamorph to reach sexual maturity. Years at age 1 are then estimated from the growth curve (Fig. 3), but those ages might be an underestimate for frogs that fell on the asymptotic portion of the curve because they were recorded as being 10 yr old at first capture even though they could have been older.

| PIT[a] no. | Sex | First capture | Length 1 (cm) | Length 2 (cm) | Weight 1 (g) | Weight 2 (g) | Interval (d) | Interval (yr) | Est. age 1 | Est. age 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| 32E11 | male | 18 September 2003 | 6.8 | 6.2 | 33.1 | 36.5 | 2504 | 6.9 | 10 | 16 |
| 13C13 | male | 06 September 2003 | 6.9 | 6.9 | 33.1 | 35.0 | 2132 | 5.8 | 10 | 16 |
| E0634 | female | 05 September 2003 | 7.7 | 7.3 | 48.0 | 47.3 | 2133 | 5.8 | 10 | 16 |
| 14A24 | female | 25 August 2003 | 7.7 | 8.1 | 59.6 | 48.0 | 2562 | 7.0 | 10 | 16 |
| 06D2E | female | 05 September 2003 | 7.2 | 7.5 | 44.0 | 49.1 | 2134 | 5.8 | 9 | 15 |
| 31001 | female | 19 August 2003 | 7.6 | 7.5 | 48.6 | 43.0 | 1431 | 3.9 | 10 | 14 |
| 45D5F | female | 21 August 2003 | 8.2 | 8.2 | 63.5 | 58.2 | 1428 | 3.9 | 10 | 14 |
| 83E12 | female | 17 September 2003 | 7.9 | 8.1 | 56.5 | 49.9 | 1400 | 3.8 | 10 | 14 |
| 90768 | female | 18 September 2003 | 6.6 | 7.5 | 28.8 | 50.2 | 2519 | 6.9 | 8 | 14 |
| 92633 | female | 19 August 2003 | 7.5 | 7.4 | 48.0 | 27.7 | 1802 | 4.9 | 10 | 14 |
| 80C56 | male | 24 August 2005 | 6.8 | 6.4 | 34.0 | 34.5 | 1798 | 4.9 | 10 | 14 |
| 0746B | female | 27 July 2005 | 7.4 | 7.5 | 46.6 | 49.0 | 1855 | 5.1 | 10 | 14 |
| 22128 | female | 04 August 2004 | 7.5 | 7.9 | 56.0 | 42.5 | 1448 | 4.0 | 10 | 14 |
| 34739 | female | 17 July 2007 | 7.4 | 7.9 | 39.0 | 55.0 | 1507 | 4.1 | 10 | 14 |
| 34772 | male | 24 July 2007 | 6.8 | 6.2 | 30.2 | 31.1 | 1472 | 4.0 | 10 | 14 |

[a] PIT = passive integrated transponder.

### *Frog Movements*

On 428 occasions involving 225 frogs, we recaptured the same individual on consecutive days. Excluding movement distances of zero (61 occasions), the median daily distance moved between captures was 8.6 m (range = 1–164 m) with only two frogs moving >100 m and seven others moving >50 m. Little evidence existed for an effect of SVL on daily distance moved, though there was a slight tendency for longer (presumably older) individuals to move greater distances (Fig. 4, Table 7a).

On 362 occasions involving 235 frogs, we recaptured the same individual in consecutive years; these data were used for analysis of annual movements. Median distance moved from one year to the next was 84 m (range = 1–1365 m). Interannual movement distances did not vary with sex or SVL (posterior probability of null model = 0.997 for annual movement distance).

We captured 76 individual frogs five or more times during the same season (median = 6, max = 14) and used those frogs to calculate seasonal MCPs. The median annual 100% MCP was 139 $m^2$ (range = 1.5–5380 $m^2$) with little variation among frogs attributable to sex or SVL (Fig. 5, Table 7b).

Frogs often occupied different areas from year to year. The seven individuals for which 100% MCPs could be estimated in more than 1 yr varied in site fidelity with the tendency to return and reuse previously occupied habitats (Switzer, 1993). Annual summer home range

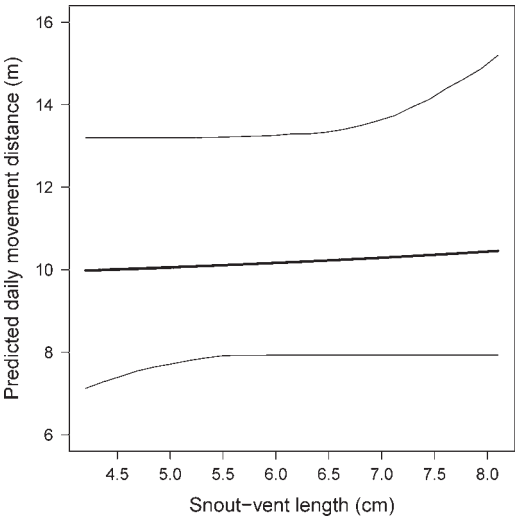


FIG. 4.—Annual (summer) daily distance moved by *Rana sierrae* as a function of snout–vent length (SVL), 2003–2011. Thin lines indicate the 95% symmetric credible interval of the predicted mean daily movement distance.

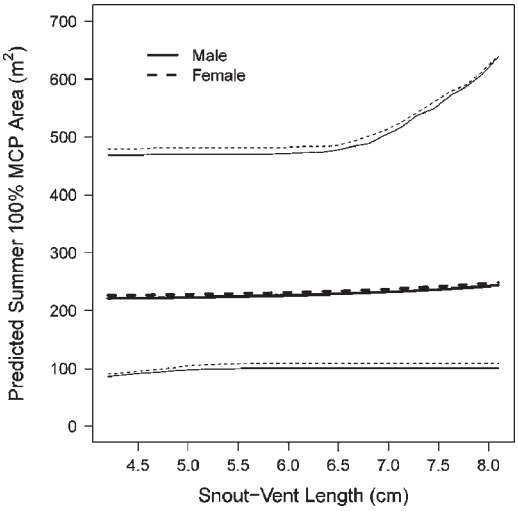


FIG. 5.—Seasonal (summer) 100% MCP summer home ranges for *Rana sierrae* as a function of snout–vent length (SVL) and sex, 2003–2011. Thin lines indicate the 95% symmetric credible interval of the predicted mean 100% MCP.

centroids moved a median of 47.7 m (range = 6.6–487.1 m), and initial 100% MCPs overlapped subsequent MCPs by a median of only 0.4% (range = 0.0–17.7%; Table 8).

## DISCUSSION

*Rana sierrae* population size estimates were variable between years, ranging from 44–115 with a mean of 86 adult frogs over the 9 yr of our study (2003–2011). There was no clear decline as might be expected based on reports that *R. sierrae* have been extirpated from 92.5% of their historic sites (Vredenburg, 2007). While there is an important difference between loss of populations and declines in population size at specific sites, one would expect to see local population declines if the range-wide trend indicates high rates of population extirpation. The persistence of the Summit Meadow population we studied is interesting and important in itself, but it is especially significant because of its long history of *Bd* infection (Fellers et al., 2011). However, infection intensity is low, ranging from 1–190 zoospore equivalents among frogs that tested positive. Even the most heavily infected frog was below (by a factor of >50) the intensity Vredenburg et al. (2010) reported as a threshold before population declines were observed in *R. sierrae* and *R. muscosa*.

TABLE 7.—Model selection results for the effects of sex and snout–vent length on movements and summer home range for *Rana sierrae* at Yosemite National Park. Intervals over which no movement occurred were omitted from the analysis. A "1" indicates that the parameter was included in the model; a "0" indicates that the parameter was not included. Models are listed in order of decreasing support. Only those models with a posterior probability ≥0.001 are included.

| Parameter | | | |
|---|---|---|---|
| Sex | SVL | Sex × SVL | Posterior probability |
| Daily movement distance | | | |
| 0 | 0 | 0 | 0.924 |
| 0 | 1 | 0 | 0.074 |
| 1 | 0 | 0 | 0.002 |
| Summer home range | | | |
| 0 | 0 | 0 | 0.924 |
| 0 | 1 | 0 | 0.041 |
| 1 | 0 | 0 | 0.035 |

We do not know the population size prior to *Bd* occurrence, but our recapture data on *Bd* negative versus positive frogs suggested that *Bd* infection might reduce the mean number of days between first and last capture (611 versus 312 d), though this trend was not significant in our data. How *Bd* infection translates to population size or vulnerability to extirpation is uncertain. If the population is at carrying capacity, the effect might be little or none. However, the population size might be depressed due to reduced survival of *Bd*-positive frogs. We are continuing to collect data on the *Bd* status of individual frogs over multiple years to address this question.

Population size varied on an annual basis. Annual population fluctuations were strongly correlated with differences in annual precipitation. There was a 2-yr lag between low precipitation and low *R. sierrae* population size and vice versa (Fig. 2). We believe the lag reflects poor survival of recently metamorphosed subadult frogs in dry years and, hence, reduced recruitment into the population 2 yr after low precipitation years. Recent metamorphs are small (2.0–2.5 cm) and readily desiccate due to their small size; hence, they need to remain near water as they begin to metamorphose during the summer. This concentrates these small frogs along the

TABLE 8.—Annual changes in space use by *Rana sierrae* at Yosemite National Park, 2003–2011. MCP = 100% minimum convex polygon (MCP) estimates; Interval = number of years between MCP estimates; Centroid change = distance between annual MCP centroids; Area of overlap = area of intersection of MCPs; Percent overlap = percent of initial MCP overlapped by subsequent MCP.

| Frog ID | Sex | Initial MCP area ($m^2$) | Subsequent MCP area ($m^2$) | Interval (yr) | Centroid change (m) | Area of overlap ($m^2$) | Percent overlap |
|---|---|---|---|---|---|---|---|
| 453F7A361A | female | 97.0 | 187.5 | 2 | 47.7 | 0.4 | 0.2 |
| 45562E7531 | female | 810.5 | 2361.5 | 1 | 33.4 | 417.9 | 17.7 |
| 465A49711D | female | 480.0 | 109.0 | 1 | 74.4 | 0.0 | 0.0 |
| 985153000001719 | male | 39.0 | 88.5 | 1 | 6.6 | 9.0 | 10.2 |
| 985153000037518 | male | 43.0 | 80.0 | 1 | 487.1 | 0.0 | 0.0 |
| 985153000042425 | female | 95.5 | 24.5 | 1 | 277.9 | 0.0 | 0.0 |
| 985153000042444 | male | 3057.0 | 113.0 | 1 | 36.7 | 91.4 | 3.0 |

muddy margins of pools that often have little cover and where Western Terrestrial Garter Snakes (*Thamnophis elegans*) and birds can easily feed on them. In wet years metamorphs can more readily move into the surrounding vegetation and perhaps have better foraging options as well.

Temporary emigration could occur if meadow conditions change and frogs move to a different part of the study area, if a frog is behaving in a way that reduces detection or if a frog occupies a site within the study area where it is hard to detect. We found that temporary emigration occurred and that it varied among primary capture periods. This was not surprising because the study area is a complex mosaic of meadows and pools along a stream corridor that is flooded in the early spring and then dries up over the summer. During early sampling sessions there were areas of flooded sedges that provide good cover and foraging for frogs, but frogs in those areas were harder to find and catch; those individuals had lower capture probabilities. As the meadow dried, frogs moved to pools where they were easier to find and effectively immigrated into the population.

*Rana sierrae* survival at our study site differed only slightly by sex, with females having marginally higher survival. Survival is often significantly lower in male anurans (e.g., *Rana grylio*; Wood et al., 1998), and this is typically attributed to the higher cost of breeding for male frogs. Perhaps the similar survival rates between male and female *R. sierrae* reflects the fact that habitat utilization is similar between sexes whereas, in many ranid frogs, males spend much of the breeding season at breeding sites while females visit those sites only briefly before returning to nonbreeding areas (e.g., *R. capito*, *R. clamitans*, *R. draytonii*, and *R. sevosa*; Lannoo, 2005) where exposure to predation may be less or where male–male competition may increase mortality rates (Arak, 1983).

Year-to-year survival of *R. sierrae* at Summit Meadow was variable, ranging from 44.6% to 95%. High overwinter survival (89%) was also reported for *R. sierrae* by Pope and Matthews (2001) over the one winter of their study. Miaud et al. (1999) found that both male and female *R. temporaria* had 80% survival at their montane study site in the French Alps at an elevation similar to ours (2300 m). One might suspect that overwintering survival in areas with significant snowfall would be related to the harshness of the winter, but Elmberg (1990) did not find such a relationship in his 10-yr study of *R. temporaria* in Sweden, so it is likely that studies specifically designed to elucidate this point will be required.

*Rana sierrae* growth and longevity at our relatively low-elevation study area (2200 m) were similar to *R. sierrae* in other parts of the Sierra Nevada. Matthews and Miaud (2007) looked at size and growth of *R. sierrae* (12 sites) and *R. muscosa* (one site) spread across 422 km of the Sierra Nevada with a weighted mean elevation of 2788 m (1509 to 3501 m elevational range). The mean SVL of frogs in their study was essentially the same as ours, while our frogs were lighter by 1.5 g for males and 3.1 g for females. This is quite similar given the broad geographic and elevational range of their study and the fact that one of their populations is now considered a closely related but separate species. Though the differences were small, they follow the trend

noted by Morrison and Hero (2003) for 12 species of anurans and one salamander, where high-altitude and high-latitude amphibians are generally larger than low-altitude or low-latitude counterparts.

Shine (1979) reported that in 90% of 668 amphibian species, females were larger than males. This trend held true in ranid frogs where males were larger than females in only 3 of 149 species. *Rana sierrae* in our study, as well as that of Matthews and Miaud (2007), followed the same pattern with females being significantly larger. Sexual dimorphism in anurans has been attributed to a slower growth rate in males (Monnet and Cherry, 2002), and this has been documented for a number of ranids (e.g., *Rana cascadae*; Briggs and Storm, 1970; *Rana grylio*, Ugarte et al., 2007). Growth rates for *R. sierrae* at our study site ($K = 0.73$ for males and 0.78 for females) were much higher than those reported by Matthews and Miaud (2007) for *R. sierrae* – *R. muscosa* ($K = 0.41$ for males, 0.50 for females). However, Matthews and Miaud did not include juveniles in their growth curves, so their ages 0 and 1 do not include the smallest individuals; thus, at each age they added the smaller individuals that just matured, making the growth look slower.

Similar to *R. sierrae*, the Anatolian Mountain Frog (*Rana holtzi*) lives in high alpine lakes in the Bolkar Mountains of southern Turkey at an elevation of 2560 m (Miaud et al., 2007). At their Lake Karagöl study site, the lake is covered with ice and snow for 5–7 mo of the year (Miaud et al., 2007), similar to Summit Meadow. However, the lake is clear with low phyto- and zooplankton biomass. This contrasts with our study site where water in the stream and meadow pools is only moderately clear and has an obvious growth of plankton along with a diversity of invertebrate prey. Juvenile *R. holtzi* attain sexual maturity at 4–5 yr, about a year later than for *R. sierrae*. *Rana holtzi* growth rates were $K = 0.26$ for males and $K = 0.18$ for females. This is significantly slower than for the *R. sierrae* we studied even though the study sites were at similar elevations. We cannot say whether differences in apparent food availability account for differences in growth, but this could be examined by comparing growth and food availability at populations of *R. sierrae* in different settings in the Sierra Nevada. Due to individual variation in growth and the fact that *R. sierrae* reach full size relatively quickly, size is probably a good indicator of age for only the first few years after reaching sexual maturity.

We calculated the maximum longevity of *R. sierrae* as 15 yr for females and 16 yr for males. This is unusually long for a ranid frog or for any anuran. Matthews and Miaud (2007) reported longevities of 13–14 yr for female and 11–12 yr for male *R. sierrae*. No other North American ranid frog has been reported to have greater longevity (Lannoo, 2005). *Rana sierrae* longevities are similar to *Bufo canorus*, another high elevation anuran that is also endemic to the Sierra Nevada; Kagarise Sherman and Morton (1984) estimate that female *B. canorus* may live up to 15 yr and males to 12 yr. Longevity has not been reported for *P. regilla*, the only other widespread anuran throughout the range of *R. sierrae*, but longevity beyond 3 yr has not been reported in any *Pseudacris* (Lannoo, 2005). The fact that both *B. canorus* and *R. sierrae* are largely inactive through the winter months may play a role in their longevity, though extended winters likely pose their own challenges. Delayed maturity is also likely to be a contributing factor. *Bufo canorus* tadpoles metamorphose in about 60 d (Kagarise Sherman, 1980; Kagarise Sherman and Morton, 1984), unlike the 2.5 yr for *R. sierrae*, but female *B. canorus* do not breed for 4–6 yr and males delay breeding for 3–5 yr (Kagarise Sherman, 1980). While the time from egg to breeding adult is not quite as long as the 6 yr for *R. sierrae*, this is still a significant delay that may contribute to their longevity.

Within a season, *R. sierrae* at Summit Meadow were sedentary, though larger frogs moved slightly more than smaller frogs. Matthews and Pope (1999) examined movement patterns of 24 radio-tagged *R. sierrae* and tracked them every 1–3 d for 1 mo at a high elevation (3470 m) site in a granite basin at the southern part of the frog's range. During August, 10 female frogs moved an average of 15.4 m/day, which was greater than the 8.6 m/day in our study. The longest within-season movement we recorded was 1039 m over 29 d. This is similar to the

movements of *R. sierrae* elsewhere within their range (1 km, Pope and Matthews, 2001; 880 m, Knapp et al., 2007) even though we did not sample during the fall when frogs move to overwintering sites (Matthews and Pope, 1999). Similarly, the summer home ranges we measured were much smaller than those Matthews and Pope (1999) measured for *R. sierrae* in August (139 $m^2$ versus 385 $m^2$). This probably relates to a difference in field techniques (radio telemetry versus our mark–recapture), length of study, a difference in analytical techniques (adaptive kernel versus our 100% MCP), and differences in behavior related to markedly different habitats in the respective study areas. Our analysis of summer home range overlap suggests that there is no strong site fidelity between years, with frogs centering their activity in somewhat different parts of the wet meadow–stream complex from one year to the next.

In summary, we report here on a population of *R. sierrae* at a relatively low elevation and in a meadow–stream complex that differed greatly from other *R. sierrae* populations that have been studied at high elevation ponds and lakes in largely barren regions of the Sierra Nevada. Our study was also unusual in lasting 9 yr and including a large number of captures (2431) of 757 individual frogs. Frogs tended to have high overwinter survival, live a long time (up to 16 yr), and grow at a fast rate, especially compared with high elevation populations of *R. sierrae*. Frogs at our study site tended to be sedentary during a given summer but had low site fidelity in subsequent years. The population size ranged from an estimated 45 to 115 adult frogs, but there was no downward trend as might be expected from recent work with other *R. sierrae* populations; this was in spite of a long history of *Bd* infection at our study site.

*Acknowledgments*.—Yosemite National Park provided logistical support and a scientific research permit. J. Dhundale, C. Dodge, D. Drake, D. Pratt, R. Stoelting, and L. Wood assisted with field work. D. E. Green confirmed the presence of *Bd* in two *R. sierrae* and C. Briggs provided unpublished data on the presence of *Bd*. P. Moore provided valuable information on the identification of meadow vegetation. C. Drost and J. Fellers provided useful comments on the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government. This is contribution 438 of the US Geological Survey Amphibian Research and Monitoring Initiative.

## Literature Cited

Arak, A. 1983. Male–male competition and mate choice in anuran amphibians. Pp. 181–210 in P. Bateson (Ed.) Mate Choice. Cambridge University Press, UK.

Briggs, C.J., R.A. Knapp, and V.T. Vredenburg. 2010. Enzootic and epizootic dynamics of the chytrid fungal pathogen of amphibians. Pp. 9695–9700 in Proceedings of the National Academy of Sciences 107, United States.

Briggs, J.L., and R.M. Storm. 1970. Growth and population structure of the cascade frog, *Rana cascadae* Slater. Herpetologica 26:283–300.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach. Springer–Science + Business Media, LLC, USA.

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modeling 197:516–519.

Cowman, D.F. 2005. Pesticides and amphibian declines in the Sierra Nevada mountains, California. Ph.D. Dissertation. Texas A&M University, USA.

Drost, C.A., and G.M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the Sierra Nevada. Conservation Biology 10:414–425.

Eaton, M.J., and W.A. Link. 2011. Estimating age from recapture data: Integrating incremental growth measures with ancillary data to infer age-at-length. Ecological Applications 21:2487–2497.

Elmberg, J. 1990. Long-term survival, length of breeding season and operational sex ratio in a boreal population of common frogs *Rana temporaria*. Canadian Journal of Zoology 68:121–127.

Fellers, G.M., D.E. Green, and J.E. Longcore. 2001. Oral chytridiomycosis in mountain yellow-legged frogs (*Rana muscosa*). Copeia 2001:945–953.

Fellers, G.M., R.A. Cole, D.M. Reinitz, and P.M. Kleeman. 2011. Amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) in coastal and montane California anurans. Herpetological Conservation and Biology 6:383–394.

Gelman, A., J.B. Carlin, H.S. Stern, and D.B. Rubin. 2004. Bayesian Data Analysis. Chapman and Hall, USA.

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

Kagarise Sherman, C. 1980. A comparison of the natural history and mating system of two anurans: Yosemite toads (*Bufo canorus*) and black toads (*Bufo exsul*). Ph.D. Dissertation, University of Michigan, USA.

Kagarise Sherman, C., and M.L. Morton. 1984. The toad that stays on its toes. Natural History 93:72–78.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Kéry, M. 2010. Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, USA.

Knapp, R.A., and F. Matthews. 2000. Non-native fish introductions and the decline of the mountain yellow-

legged frog from within protected areas. Conservation Biology 14:428–439.

Knapp, R.A., D.M. Boiano, and V.T. Vredenburg. 2007. Removal of nonnative fish results in population expansion of a declining amphibian (mountain yellow-legged frog, *Rana muscosa*). Biological Conservation 135:11–20.

Kuo, L., and B. Mallick. 1998. Variable selection for regression models. Indian Journal of Statistics 60:65–81.

Lannoo, M.J. (Ed.). 2005. Amphibian Declines: The Conservation Status of United States Species. Volume 2: Species Accounts. University of California Press, USA.

Matthews, K.R., and C. Miaud. 2007. A skeletochronological study of the age structure, growth, and longevity of the mountain yellow-legged frog, *Rana muscosa*, in the Sierra Nevada, California. Copeia 2007:986–993.

Matthews, K.R., and K.L. Pope. 1999. A telemetric study of the movement patterns and habitat use of *Rana muscosa*, the mountain yellow-legged frog, in a high-elevation basin in Kings Canyon National Park, California. Journal of Herpetology 33:615–624.

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

Mazerolle, M.J., L.L. Bailey, W.L. Kendall, J.A. Royle, S.J. Converse, and J.D. Nichols. 2007. Making great leaps forward; accounting for detectability in herpetological field studies. Journal of Herpetology 41:672–689.

Miaud, C., R. Guyétant, and J. Elmberg. 1999. Variations in life-history traits in the common frog *Rana temporaria* (Amphibia: Anura): A literature review and new data from the French Alps. Journal of Zoology 249:61–73.

Miaud, C., N. Üzüm, A. Avci, and K. Olgun. 2007. Age, size and growth of the endemic Anatolian mountain frog *Rana holtzi* from Turkey. Herpetological Journal 17:167–173.

Monnet, J.-M., and M.I. Cherry. 2002. Sexual size dimorphism in anurans. Pp. 2301–2307 in Proceedings of the Royal Society of London B 269.

Morrison, C., and J.-M. Hero. 2003. Geographic variation in life-history characteristics of amphibians: A review. Journal of Animal Ecology 72:270–279.

Peng, R., D. Murdoch, B. Rowlingson, and M. Alan. 2010. gpclib: General polygon clipping library for R: An online reference. Available at http://www.cs.man.ac.uk/~toby/alan/software/. Archived by WebCite at http://www.webcitation.org/65ziptYJE on 7 March 2012.

Pollock, K.H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:757–760.

Pope, K.L., and K.R. Matthews. 2001. Movement ecology and seasonal distribution of mountain yellow-legged frogs, *Rana muscosa,* in a high-elevation Sierra Nevada basin. Copeia 2001:787–793.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Austria. Available at http://www.R-project.org/. /. Archived by WebCite at http://www.webcitation.org/65zj9NrIh) on 7 March 2012.

Royle, J.A., and R.M. Dorazio. 2008. Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities. Academic Press, UK.

Schmidt, B.R., and J. Pellet. 2009. Quantifying abundance: Counts, detection probabilities, and estimates. Pp. 465–479 in C.K. Dodd, Jr. (Ed.), Amphibian Ecology and Conservation: A Handbook of Techniques. Oxford University Press, USA.

Shine, R. 1979. Sexual selection and sexual dimorphism in amphibia. Copeia 1979:297–306.

Sodhi, N.S., D. Bickford, A.C. Diesmos, T.M. Lee, L.P. Koh, B.W. Brook, C.H. Sekercioglu, and C.J.A. Bradshaw. 2008. Measuring the meltdown: Drivers of global amphibian extinction and decline. PLoS ONE 3:e1636.

Sparling, D.W., and G.M. Fellers. 2007. Comparative toxicity of Chlorpyrifos, Diazinon, Malathion and their oxon derivatives to *Rana boylii*. Environmental Pollution 147:535–539.

Sparling, D.W., and G.M. Fellers. 2009. Toxicity of two insecticides to California, USA, anurans and its relevance to declining amphibian populations. Environmental Toxicology and Chemistry 28:1696–1703.

Sparling, D.W., G.M. Fellers, and L.L. McConnell. 2001. Pesticides and amphibian declines in California, USA. Environmental Toxicology and Chemistry 20:1591–1595.

Spiegelhalter, D.J., A. Thomas, N. Best, and D. Lunn. 2003. WinBUGS Version 1.4 User Manual. MRC Biostatistics Unit, Cambridge, U.K. Available at http://www.mrc-bsu.cam.ac.uk/bugs. Archived by WebCite at http://www.webcitation.org/65zjJ3bY7) on 7 March 2012.

Spiegelhalter, D.J., A. Thomas, N. Best, and D. Lunn. 2011. OpenBUGS User Manual Version 3.2.1. MRC Biostatistics Unit, UK.

Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: A package for running WinBUGS from R. Journal of Statistical Software 12:1–16.

Switzer, P.V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533–555.

Ugarte C.A., K.G. Rice, and M.A. Donnelly. 2007. Comparison of diet, reproductive biology, and growth of the pig frog (*Rana grylio*) from harvested and protected areas of the Florida everglades. Copeia 2007:436–448.

Vredenburg, V.T. 2007. Concordant molecular and phenotypic data delineate new taxonomy and conservation priorities for the endangered mountain yellow-legged frog (Ranidae: *Rana muscosa*). Journal of Zoology 271:361–374.

Vredenburg, V.T., R. Bingham, R. Knapp, J.A.T. Morgan, C. Moritz, and D. Wake. 2006. Concordant molecular and phenotypic data delineate new taxonomy and conservation priorities for the endangered mountain yellow-legged frog. Journal of Zoology 271:361–374.

Vredenburg, V.T., R.A. Knapp, T.S. Tunstall, and C.J. Briggs. 2010. Dynamics of an emerging disease drive large-scale amphibian population extinctions. Pp. 9689–9694 in Proceedings of the National Academy of Sciences 107.

Wagner, N., J. Pellet, S. Lötters, B.R. Schmidt, and T. Schmitt. 2011. The superpopulation approach for estimating the population size of 'prolonged' breeding amphibians: Examples from Europe. Amphibia–Reptilia 32:323–332.

White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Wood, K.V., J.D. Nichols, H.F. Percival, and J.E. Hines. 1998. Size-sex variation in survival rates and abundance of pig frogs, *Rana grylio*, in northern Florida wetlands. Journal of Herpetology 32:527–535.

Zweifel, R.G. 1955. Ecology, distribution and systematics of frogs of the *Rana boylii* group. University of California Publications in Zoology 54:207–292.

*Accepted:* 27 February 2013
*Associate Editor:* Rulon Clark