Response of At-Risk High-Elevation Amphibians and Their Habitat to Severe Drought Conditions

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INTRODUCTION

Amphibians are among the most susceptible taxa to extended drought conditions because of their reliance on aquatic habitats. Species that breed in shallow, ephemeral waters and species that rely on the presence of surface water for all life stages are particularly vulnerable. California has suffered from a severe drought since 2012 with unprecedented low snowpack levels in the Sierra Nevada and Cascade Range in 2015. The effects of extended drought on native amphibians in these areas are unknown. We investigated the effects of the California drought on populations and habitats of three montane frog species in the Sierra Nevada and Cascade Range, CA: the Yosemite toad (*Anaxyrus canorus*), the Sierra Nevada yellow-legged frog (SNYLF, *Rana sierrae*), and the Cascades frog (*Rana cascadae*).

The Yosemite toad, endemic to the Sierra Nevada, is listed as threatened under the Endangered Species Act (USFWS 2014) and is a California state species of special concern. The Yosemite toad is particularly sensitive to drought because it breeds in wet meadows in very shallow, ephemeral water, often less than 4 cm deep (Karlstrom 1962, Kagarise Sherman 1980, Brown et al. 2012). Successful recruitment requires persistence of this shallow water for sufficient duration into the summer for tadpoles to metamorphose. Drought may eliminate, reduce the extent, or increase the desiccation rates of these shallow water habitats. The Cascades frog is a California state species of special concern, and its federal listing status is currently under review. The Cascades frog has declined precipitously in the southern Cascade Range of California, and it now persists almost exclusively in shallow wet meadow habitats. The frog is highly aquatic and needs permanent surface water for all life stages. The federally endangered and state threatened SNYLF is endemic to the Sierra Nevada and is highly aquatic for all life stages. The SNYLF requires perennial water for its multi-year tadpole stage. Due to the widespread presence of nonnative trout throughout its range, many SNYLF populations are now relegated to small and/or shallow habitats that are generally less than 1 hectare in surface area and/or less than 2-3 meters in maximum depth. These smaller habitats are susceptible to substantial or complete drying during drought and may be more likely to completely freeze over the winter.

We examined how drought may impact these species by (1) investigating the hydrogeomorphology of Yosemite toad and Cascade frog meadows to identify habitats that may be vulnerable to changing conditions and (2) resurveying known occupied meadows, lakes, and streams for Yosemite toad and SNYLF.

For the Yosemite toad and Cascades frog, meadow hydrology is a key component of high quality habitat. Many meadows in the Sierra Nevada, however, have been degraded resulting in the deterioration and loss of these shallow water habitats and potentially contributing to the decline of these species. The mechanisms of how hydrologic and geomorphic processes form Yosemite toad and Cascades frog habitat have not been described or quantified. More specifically, the hydrologic and geomorphic factors controlling the relationship between surface

water conditions and suitable breeding habitat are not known. Understanding the links between climate, groundwater, and surface water in meadows is critical for identifying habitat that may be vulnerable to changing conditions, and in turn, developing effective conservation options.

For the Yosemite toad and SNYLF, the USFS surveyed numerous meadows, lakes and streams located on national forest lands throughout the range of the species from seven to nine consecutive years from 2002-2010 (Brown et al. 2012, Brown and Olsen 2013, Brown et al. 2014). These provide a robust pre-drought baseline of species occupancy for evaluating how the drought may have impacted these species.

DROUGHT EFFECTS ON THE HYDROGEOMORPHOLOGY OF AMPHIBIAN HABITAT

Sierran Meadows

Methods and Analysis

A Forest Service collaborative study with the Sierra National Forest, USFS Sierra Nevada Amphibian Monitoring Program, and Pacific Southwest Research Station was implemented in 2009 to better understand the breeding patterns of the Yosemite toad associated with the hydrology and water quality of meadows in the Bull Creek Watershed on the Sierra National Forest (Figure 1). This area was selected because of the long-term research ongoing at the Kings River Experimental Watersheds (KREW). In this watershed, we have monitored surface water extent, depth to groundwater, and Yosemite toad breeding success in five meadows from 2009 through 2016. This time period encompassed wet, normal, and dry water years providing insights for how snowpack levels and drought affect the hydrology of Yosemite toad habitats. In 2016, we further instrumented one of these meadows, 520M15, to collect additional hydrologic and topographic data, and added two meadows to the larger study. In this report, we present results for 520M15 because it has both historical data for assessing trends during the drought and detailed hydrogeomorphic data to assess the influence of meadow hydrology on breeding habitats.

Within each Bull Creek meadow, two occupied and two unoccupied (potential) breeding areas were randomly selected based on surveys conducted after snowmelt from 2006-2008 as part of bioregional amphibian monitoring (see Brown et al. 2012). Potential breeding areas were defined as contiguous surface water $\geq 1m^2$ with $\leq 50\%$ visibly moving water. We established two transects of wooden stakes (spaced 2 m apart) that ran along the greatest longitudinal and cross-sectional axes of each selected breeding and nonbreeding area. On the downslope side of each stake, we recorded the depth of water. For analysis we defined presence of water as any water > 0.005 m in depth. The percent of stakes with water presence was calculated to quantify relative surface water area.

We installed transects of monitoring wells cross-sectional to the longitudinal axis of each meadow on the upslope side of each selected breeding and nonbreeding area. To measure seasonal changes in depth to groundwater, three to seven monitoring wells were placed on each transect at the lowest topographic point, mid-slope between the lowest point and forest edge on each side, and at each forest edge (see Figure 1 for 520M15 example). One of the monitoring wells was placed on the upslope side of each breeding or nonbreeding area.

Approximately every 2 weeks from snowmelt to early September in most years, we measured surface water depths at the stakes, recorded depth to ground water in the wells, and conducted visual encounter surveys (VES, Crump and Scott 1994, Olson et al. 1997) for Yosemite toads. VES were conducted for the entire meadow, recording relative abundance of each life stage both within and outside of each selected breeding area. The resolution of the relative abundance data determined whether only a few, tens, hundreds, or thousands of individuals were found. We used these data to document the presence and timing of metamorphosis.

We used simple descriptive statistics and graphics to compare changes in depth to groundwater and surface water extent across years prior to and during the drought. We examined depth to groundwater and groundwater temperature data in 2016 in meadow 520M15 to investigate water sources and patterns across the season to better understand potential influences on Yosemite toad breeding areas.

Lastly, we installed two time lapse cameras in 520M15, one overlooking the meadow to document snowmelt patterns, and one focused on a breeding microsite as a test of potential remote methods for monitoring surface water conditions. One Moultrie game-cam was installed on March 1, 2016 prior to snowmelt, and images were assessed for snowmelt patterns across the meadow. A second Moultrie game-cam was installed in June 2016 to determine if surface water extent in a breeding microsite could be assessed remotely. Both cameras were set to record hourly images through August 2016, and images were assessed for surface water presence.

Results

Groundwater and Surface Water Trends Prior to and During the Drought

Figures 2 and 3 show trends in water table depths and surface water area from 2009 to 2016 at the four sampled breeding and nonbreeding areas in meadow 520M15. From 2009 through 2011, water table levels remained near the surface at all sites, while surface water fluctuated depending on snowpack and site. In the two breeding areas, surface water area declined through the summer during 2009 when April 1 snowpack in the southern Sierra was 78% of normal. 2010 and 2011 had average (105%) and above average (161%) snowpacks, respectively, and surface water remained present for sufficient duration for metamorphosis to occur. The two unoccupied areas generally had less surface water.

In 2012, the first year of the drought with April 1 snowpack at 37% of normal, water tables generally remained high, but there was very little surface water, even in the spring. Water tables started declining in 2013 (snowpack at 47% of normal), and continued to decline in 2014 (snowpack at 33% of normal) to the point that monitoring wells were dry at some point during the summer at all breeding and nonbreeding areas except 009. Monitoring wells were completely dry at 002 and 005 in 2015, even at snowmelt. The snowpack in 2015 was an unprecedented 5% of normal. In 2014 and 2015, two years into the drought, there was almost no surface water in the meadow.

Meadow 520M15



Figure 1. Meadow 520M15 showing locations of monitoring wells (shown by blue circles) and breeding and nonbreeding areas (shown by purple polygons). Long-term monitoring data exists for breeding areas 002 and 024 and nonbreeding areas 005 and 009. Additional breeding areas 015 and 050 and nonbreeding areas 060 and 062 were added in 2016. The aerial image in the background was flown in August 2015 by a small drone quadcopter.



Figure 2. Seasonal and annual trends in depth to water table and surface water extent from 2009-2016 at two occupied breeding areas, 002 and 024, in meadow 520M15 in Bull Creek, Sierra National Forest. Breeding dates and the dates metamorphs were first observed are shown on surface water graphs.



Figure 3. Seasonal and annual trends in depth to water table and surface water extent from 2009-2016 at two nonbreeding surface water areas, 005 and 009, in meadow 520M15 in Bull Creek, Sierra National Forest.

In 2016, the April 1 snowpack level was 78%, which, although still less than normal, was higher than had occurred the previous four years. We observed surface water in the breeding areas and other parts of the meadow, but many areas of the meadow were dry, and locations with surface water dried quickly. Depth to water table in the wells were similar to depths observed in 2012, the first year of the drought.

Yosemite toad breeding responses generally followed the drought trends. Egg masses were laid and metamorphs observed every year from 2009-2011. In 2012, the first year of the drought, eggs were laid but successful metamorphosis was not observed. In 2013, males did not form their typical breeding chorus in spring and no eggs were found. A distinct snowmelt period was not observed in 2013 as had typically been observed in prior years, and very little surface water habitat was present. In 2014 and 2015, 520M15 was completely dry, even at snowmelt, and no toads were found during spring surveys. Yosemite toad breeding activity in 2016 was more similar to predrought years; we observed toads breeding, found egg masses and, despite rapidly drying conditions in the meadow, observed toads reaching metamorphosis in late summer.

Groundwater Patterns in 2016

We further examined spatial groundwater patterns and temperatures across 520M15 meadow in 2016 to better understand the potential influences of meadow hydrology on Yosemite breeding habitats. Groundwater levels remained high (<0.2 m depth) in the central portion of the meadow on both transects 3 and 4 (near wells 3B, 4B and 4C, Figure 4) throughout the year indicating a consistent groundwater input at the top center of the meadow (Figure 4). Depth to groundwater was greater and decreased over the season at the meadow edges (wells 3A, 3C, 4A, 4F) and at well 4D near the western edge of the east lobe of the meadow. This indicates that groundwater was primarily flowing from the upper central portion of the meadow downstream, rather than from the hillslopes to the channel. Manual temperature measurements taken from these wells at the time of depth measurements were consistent across the season at around 10-15 °C indicating a steady groundwater source (Figure 5).

Hourly water temperature data from loggers in monitoring well (MW) 3B and from the outlet stream at the downstream end of the meadow also indicated a shallow subsurface groundwater supply at the top of the meadow and seasonal draining of water at the downstream end. Similar to the manual well measurements in the upper portion of the meadow, the hourly temperature data in 3B was consistent remaining between 5-8 °C year-round indicating groundwater input (Figure 6). The stream temperatures reflected seasonal and diurnal fluctuations; once snowmelt occurred in May, temperatures warmed quickly to greater than 15 °C in June for most of the summer before decreasing again in early fall.

The hourly stage data from the logger in 3B indicated a rapid recharge of the groundwater following snowmelt and consistent depth across the summer season before a gradual decline in late summer. Winter storms created spikes in water level, and small daily fluctuations in stage in late summer indicate the influence of evapotranspiration. In general, the consistent water level through summer indicates shallow groundwater dominated this upper meadow area.

In the central portion of the meadow, monitoring wells along transect 5 showed similar trends to transects 3 and 4 up-gradient. Wells at the meadow edges showed a seasonal signal with increasing depth to groundwater from June to September (Figure 7), while wells 5C and 5D near the channel showed consistently high groundwater levels likely due to groundwater input from

upstream. The declines in groundwater across the season suggest water in much of the meadow was likely coming from precipitation via surface and shallow subsurface sources rather than deeper springs. Manual measurements of water temperature in transect 5 wells showed similar seasonal patterns to wells in the upper meadow in that groundwater remained around 10-12 °C for the duration of the summer (Figure 8). However, temperatures in wells 5C, 5D and 5F were notably warmer in mid-summer (18-20 °C) than the other wells. This suggests warmer surface water may have entered the groundwater pool at these locations or just upstream; however, additional information is needed to elucidate potential surface-groundwater exchanges.

At the downstream end of the meadow, manual water temperature measurements in wells on transects 6 and 7 showed similar seasonal patterns to wells in the upper meadow in that groundwater remained around 10 °C for the duration of the summer with temperatures near the channel (6C) slightly higher (13-15 °C) (Figure 9). Monitoring wells on transect 6 showed groundwater levels remained high near the channel across the season, while depth to groundwater in wells at the edge of the meadow (6E) decreased through time (Figure 10). Well 6A is located near a potential seepage area on the western hillslope where water often pools in cattle hoofprints. Depth to groundwater, however, remained consistently high across the transect suggesting groundwater from upstream dominated this area rather than seepage from the hillslope.

At the downstream end of the meadow, groundwater levels along transect 7 decreased through time suggesting water drains from the meadow slowly across the year with higher rates along the drier eastern side. These data suggest that the central portion of the meadow and to some degree the lower portion of the eastern lobe near wells 5F and 5G were dominated by shallow subsurface groundwater, while the remainder of the meadow may have been surface water-dominated.



Figure 4. Depth to groundwater from June to August 2016 at monitoring wells on transects 3 and 4 across the upper portion of the meadow. Refer to Figure 1 for well locations. Well 3A is located at the upper western side of the meadow near the forest edge, 3B is located in the center of the transect, and 3C is near the eastern side of the meadow. Wells on transect 4 follow a similar naming convention (4A is on western meadow-right side).



Figure 5. Water temperature in monitoring wells and stream channels on transects 3 and 4 from June to August 2016. (The 50 °C point is an error to be corrected). Data were collected coincident to groundwater level measurements.



Figure 6. Hourly water temperature in monitoring well (MW) 3B at the center upstream end of the meadow and in the outlet stream at the downstream end of the meadow and stage (depth) in 3B from fall 2015 through fall 2016.



Figure 7. Depth to groundwater from June to September 2016 at monitoring wells on transect 5 in the central portion of the meadow (Figure 1). MW5A is located at the downstream left side of the meadow, MW5E is at the center of the v-shaped transect, and MW5H is on the downstream right side of the meadow. Note that MW5E is plotted in both graphs for reference.



Figure 8. Water temperature in monitoring wells on transect 5 from June to September 2016.



Figure 9. Water temperature in monitoring wells on transects 6 and 7 from June to September 2016.



Figure 10. Depth to groundwater from June to September 2016 at monitoring wells on transects 6 and 7 in the downstream portion of the meadow. Refer to M15 meadow figure for well locations.

Time Lapse Cameras

In 2016, snow at meadow 520M15 melted out first in the lower and central part of the meadow longitudinally, and the central part of the meadow latitudinally (Figure 11). This includes several of the breeding areas. About half of the meadow melted out between April 1 and May 1. Breeding began approximately in mid-May of this year, and adults were present by May 13. Positioning of

the camera is important and in 2017, we plan to place this camera so it captures more of the breeding area near 002.

Surface water was difficult to see in the images from the camera placed at the bottom of breeding area 002 (Figure 12). Dense vegetation as shown in these pictures is typical of Yosemite toad breeding areas.

Imagery technology continues to improve and we plan to continue experimenting with different techniques. Developing an efficient and effective method to monitor the extent and persistence of Yosemite toad breeding habitat is a priority.

Discussion

The long-term trend data, from 2009-2016, clearly shows the effect of the extended drought on both groundwater levels and surface water extent. Depth to water table declined further with each successive year of the drought, suggesting a lag effect. One year of drought may not greatly impact groundwater, but successive years of drought appeared to result in dramatic lowering of water table depths. Surface water was not as resilient. Even in 2012, when water tables were still relatively high, surface water was greatly reduced. By the second year of the drought, there was essentially no habitat available for Yosemite toad breeding in 520M15.

The primary water source in 520M15 appears to be shallow subsurface groundwater coming in from the top of the meadow. The only surface water enters at the upstream end of the eastern lobe, and the small channel is dry most of the season. There is no surface water entering at the top of the meadow. Groundwater remains closest to the surface along the central longitudinal axis of the meadow. Interestingly, most of the primary Yosemite toad breeding areas are along this axis in the central part of the meadow. This also may be the area that melts out first in the spring due to high, relatively warm groundwater levels and movement of surface sheetflow down-gradient.

The declines in groundwater in 520M15 across the 2016 season suggest water in much of the meadow was likely coming from precipitation via surface and shallow subsurface sources rather than deeper springs. This suggests that this meadow may be more vulnerable to drought. Analysis of water quality data collected throughout the meadow and topographic variation across the meadow, which is not yet complete, will contribute to interpretation and understanding of these observed trends.

Most habitats for the Yosemite toad in this meadow occur in very shallow water (1-2 cm) flooded vegetation rather than open pools or ponds. Breeding area 002 is a sloping area with very shallow sheetflow and a slightly deeper channel along the western edge. Breeding areas 015 and 024 are flatter topographically. There are two shallow pools in this meadow where water backs up behind fallen logs. Toads will occasionally lay eggs in these pools, but they seem to prefer the more shallow vegetated areas in the meadow. Microsite 009 generally is a wet area where water tables remained high even through the drought; however, we have never observed toad breeding in this location, potentially because surface water does not pool sufficiently in this area. We are



Figure 11. Snowmelt and seasonal changes in meadow 520M15 in Bull Creek, Sierra National Forest shown by time lapse camera. The camera is placed in a tree at the bottom of the meadow.



Figure 12. Images of breeding area 002 in meadow in meadow 520M15 in Bull Creek, Sierra National Forest taken from time lapse camera to investigate alternative methods for measuring surface water extent. Surface water is difficult to see in these images.

investigating the role of topography and its interaction with surface and groundwater patterns in the formation of suitable breeding habitats.

The very shallow (1-2 cm) ephemeral water in which toads typically lay their eggs appears to be particularly susceptible to drought. Yosemite toads can be long-lived; we have documented adults as old as 13 years, assuming a 3 year subadult stage (Brown et al. unpublished data). Further, adults returned to lay eggs in 2016 once water was again available after the three years the meadow was dry. It is hypothesized that conservation of the long-lived adults is important for the persistence of Yosemite toads given their unpredictable breeding habitats. Our results support this hypothesis.

Cascade Range Meadows

Methods

Groundwater Wells

In 2015, we established ground water monitoring wells at three meadows that support Cascades frogs in the southern Cascade Range: Carter Meadow on the Lassen National Forest (Figure 13), Childs Meadow on Collins Pine Lumber Company lands (Figure 14), and Old Cow Creek on Beatty Lumber Company lands. We established at least three transects with at least three monitoring wells per transect at each meadow and also established staff and stage gauges in the primary stream channel at the top and bottom of each meadow and in channels bisected by transects (Figure 13B). In some wells in each meadow, stage and temperature loggers (Solinst levelloggers) were set to record groundwater levels and temperatures continuously. At the rest of the wells, we manually recorded water level, water temperature, and electrical conductivity (EC) every two weeks during the snow-free season. We also installed two time lapse game cameras at Carter Meadow and two in the beaver control reach of Childs Meadow to record changing snow and water levels through the wet winter season (Figure 13B).

Breeding Pool Hydrology

We have been studying several of the remaining Cascades frog populations in the southern Cascade Range in California since 2008. Using detailed population data collected over this time period, we determined that only one of these populations, in Carter Meadow, has an > 50% probability of being self-sustaining for the next 50 years (Pope et al. in prep). For this reason, in 2016 we focused most of our efforts on understanding breeding pool hydrology in relation to drought effects in Carter Meadow. We also focused efforts in Childs Meadow where we are conducting an ongoing study to assess the effects of meadow restoration using beaver dam analogues on Cascades frog population dynamics. At Childs Meadow, we studied breeding pool hydrology in our positive control reach where beavers have dammed the channels, creating breeding habitat for Cascades frogs. Unfortunately, the beavers abandoned (or were predated from) the reach during the winter of 2015/2016 and so did not repair a breach in the upper dam (Figure 14). Cascades frogs still bred in a couple flooded side pools, and we were able to monitor breeding pool surface hydrology at these pools and two paired non-breeding pools. At Old Cow Creek, the Cascades frog population has declined to only a few remaining frogs and one breeding site within a spring-fed flooded section of the meadow, so we were unable to use the meadow for the surface water breeding pool hydrology assessment.

During early season visits to the meadows, we surveyed for signs of breeding such as the presence of egg masses and tadpoles. Once a breeding pool was identified, we set up two to three transects to characterize the change in surface area and pool depth over the course of the season. We benchmarked starting and ending points of each transect so that they would remain constant throughout the season. For each breeding pool, we designated a paired non-breeding pool of similar size and depth and set up transects in the same manner. We surveyed seven pairs of pools in Carter Meadow and two pairs in Childs Meadow. Approximately every two weeks, we ran a meter tape along each transect and noted the distances from each benchmark to standing water, as well as the water depth at each meter along the transect. We measured pH, EC, and



Figure 13. (A) Location of the three Cascade Range meadows. (B) Overview of Carter Meadow with ground-mapped surface water overlaid on the image. (C) Locations of pools used by Cascades frogs (*Rana cascadae*) in Carter Meadow for breeding (green) and pools without breeding (brown) in 2016. Pools where we measured changes in surface hydrology in 2016 are represented as circles while other breeding pools are represented as triangles. Groundwater wells are represented by open circles with dots and time lapse camera stations are circles with crosses.



Figure 14. Drone image of the beaver control reach of Childs Meadow taken in the spring of 2015 when the upper beaver dam was intact and maintained by beaver. The blue arrow marks the location of the breach that occurred in the winter of 2015/2016 and was not repaired in 2016.

temperature at five random locations throughout the pool and counted Cascades frog egg masses, tadpoles, or metamorphs and noted their Gosner stages. We also drew a sketch of each pool and took pictures from each benchmark to track changes in the overall shape and size of the water body throughout the season.

Analytical Methods

We compared drawdown rates of pools to determine if there was a significant difference in groundwater influence between breeding and nonbreeding pools. Drawdown rates were calculated as the proportional differences in pool volume between the first complete high water survey (second survey, June 7th - 10th) and the first low water survey (fifth survey, August 1st - 3rd). If pools dried down completely before the fifth survey, we used the first date to calculate the drawdown rate. Pool volume was calculated by multiplying the surface area by the average depth of each transect. It was assumed that pools were oval in shape and so the formula $r_1 \times r_2 \times \pi$ was applied, where r_1 is half the wetted width of transect 1 and r_2 is half the wetted width of transect 2. When there was a third transect, the two widths (transects 2 and 3) were first averaged. To test if breeding site selection is related to drawdown rate (a surrogate for to the amount of ground water infusion), we performed a binomial mixed-effects logistic regression (lmer) in Program R, keeping meadow as a random effect. We also used mixed-effects logistic regression (glmer) to test for significant differences in pool volume and surface area between breeding and non-breeding sites.

To determine if water quality differed between breeding and nonbreeding pools, we compared the mean pH, EC, and water temperature values recorded during each survey (~5 measurements per pool per survey). We again created binomial mixed-effects models to assess the relationship between breeding status (Yes/No) in 2016 and the water quality variable while accounting for the date of the survey, the sampled meadow, the pool and its pair.

Results

Groundwater Wells

The groundwater wells provide insight into the meadow hydrology of the three Cascades frog breeding meadows. Here, we focus on Carter Meadow and Childs Meadow so that we can relate the well information to the surface water patterns observed at the breeding pools. At Carter Meadow, groundwater levels remained high (<0.5 m depth) across both transects 3 and 4 throughout the year indicating constant deep groundwater input across the upper (southern) portion of the meadow (Figure 15A). Groundwater levels remained consistently close to the surface in each of the wells and are only slightly lower (~0.25 m deep on transect 3) near the main stream channel, indicating groundwater is flowing towards the channel and the springs are the primary source of water to the meadow. Manual temperature measurements taken from the wells at the time of depth measurements also did not fluctuate much across the season and remained consistently around 10-12°C indicating a steady deep groundwater source. In the downstream (northern) portion of the meadow, monitoring wells along transects 1 and 2 show a stronger seasonal signal with increasing depth to groundwater from mid-June to September, with the exception of Monitoring Well (MW) 01-03 in the lower right (east) side of the meadow, which shows consistently high groundwater levels due to a nearby spring (Figure 15B). The wells towards



Figure 15. Depth to groundwater from March to September 2016 at monitoring wells on transects 3 (A) and 1 (B). Transect 3 crosses the upper (upstream) middle half of the meadow and transect 1 crosses the lower half of the meadow (see Figure 13B). On transect 1, MW01-03 (blue line) is on the downstream right (east) side of the meadow near where a spring enters the meadow.

the main channel and left (west) side of the meadow on transect 2 show a steeper decline (larger drop in groundwater level) through summer indicating water for this portion of the meadow is likely coming from precipitation via surface (upstream channels) and shallow subsurface sources along the western edge of the meadow rather than deeper springs. The manual measurements of water temperature in the lower meadow wells show similar seasonal patterns to wells in the upper meadow in that groundwater warms in late spring to around 10-12°C for the duration of the summer.

Five wells established adjacent to breeding areas in the central eastern and lower eastern portions of the meadow (Figure 13B) showed similar patterns to the well data in the upper and eastern portion of the meadow. The hourly temperature data in the breeding ponds fluctuated seasonally but remained below 15°C indicating consistent groundwater input (Figure 16A). Once snowmelt occurred in late April, temperatures warmed quickly from < 5°C to approximately 12°C for most of the summer before decreasing again in fall. Large diurnal swings in temperature due to surface warming, which commonly can range from 10°C to 25°C, were not evident.

The hourly stage data from the loggers near the breeding pools indicated a consistent depth across the breeding season in a well near the northeastern breeding area and a well adjacent to Infinity or Long-toed Pool in the central breeding area (Figure 16B). Interestingly, this pool was included as a surface water monitoring pool and was found to dry out before larvae had a chance to metamorphose. The other three wells showed some seasonal variation in depth with stage decreasing by about 20 cm in late summer. The pools adjacent to at least two of these wells retained water and had successful recruitment of Cascades frogs in 2016.



Figure 16. Water temperature (A) and groundwater stage (depth) (B) for five wells located near Cascades frog breeding pools in Carter Meadow from July 2015 to July 2016. Three wells are located downstream of transect 3 in the upper portion of the meadow, and two wells are located in the downstream portion of the meadow. Stage hydrographs have been adjusted to the same relative stage on June 14, 2016 to allow for comparisons in pattern and timing between sites. Winter storms create spikes in pool depth between October and April, and daily fluctuations in stage in summer indicate the influence of evapotranspiration on water levels. All pools are relatively consistent in their depths with only small (20 cm) decreases in late summer in some locations indicating groundwater sources dominate these areas.

Breeding Pool Hydrology

We used the nine paired pools where we measured changes in surface water over the course of the 2016 season to test for differences between pools used for breeding and pools not used for breeding. We conducted a mixed-effects logistic regression with Meadow as a random effect and found no significant differences in the drawdown rate between breeding and non-breeding pools (*estimate* = 1.21, p = 0.35, Table 1). We also tested for differences in pool volume and pool surface area measured during survey #2 (early June 2016). Pool volume was not significantly different between the breeding and non-breeding sites (*estimate* = -0.13, p = 0.48). Surface area was also not significant (*estimate* = -0.04, p = 0.22), nor was pool surface area to volume ratio (*estimate* = 0.01, p = 0.89). However at Childs Meadow specifically, the two breeding pools were larger in both volume and surface area than the paired non-breeding pools.

We also found no differences in pH, EC or water temperature between pools with and without breeding after controlling for meadow and survey period (Figure 17).

Table 1. Mean and standard error () of pool volume (m ³), surface area (m ²) and drawdown rates (m ³ /day),
count of pools that dried up by mid-September, and the average day they dried up, by site and breeding
status.

Site	Breeding status	Volume	Surface area	Drawdown rate	# Dried	Dry date
Carter	Breeding	2.28 (0.88)	32.56 (15.70)	0.05 (0.02)	2	7/17/2016
	Non-breeding	2.91 (1.47)	17.37 (7.34)	0.05 (0.02)	2	7/17/2016
Child's	Breeding	6.76 (0.68)	41.26 (10.72)	0.08 (0.02)	1	7/14/2016
	Non-breeding	0.71 (0.55)	12.18 (10.54)	0.05 (0.03)	2	7/06/2016



Figure 17. Binomial mixed-effects model results comparing (A) pH (*estimate* = -0.35, p = 0.85), (B) electrical conductivity (*estimate* = 0.11, p = 0.95), and (C) temperature (*estimate* = 0.46, p = 0.81) among breeding and non-breeding pools.

Discussion

We found that Carter Meadow's hydrology is primarily driven by groundwater influences while Childs Meadow's hydrology seems to be influenced by a combination of groundwater and surface flows. Groundwater wells at Carter Meadow show less fluctuations in stage, temperature and EC than at Childs Meadow suggesting a more consistent and deeper groundwater influence. Interestingly, the upper and eastern parts of Carter Meadow with the strongest groundwater influence also support the majority of Cascades frog breeding pools in the meadow (Figure 13B). Due to its deep groundwater source, surface hydrology at Carter Meadow is less likely to be affected by short-term drought conditions than other meadows such as Childs Meadow or many of the other meadows where Cascades frogs once occurred. At Childs Meadow, breeding pools were only found in association with beaver dams. Since groundwater is less of an influence in this part of the meadow, it may be that beavers provide the necessary stabilizing role by backing up surface water at a consistent elevation even if the groundwater table is dropping. In 2016, one of the beaver dams breached and water levels became less consistent causing the two primary breeding areas known from 2015 to dry and eggs to desiccate.

At the within-meadow scale we did not find any significant hydrological differences between pools found to support breeding in 2016 and pools where breeding was not found. We did pick nonbreeding pools that were nearby and similar in size to the breeding pools, but even so, we expected potential differences in drawdown rates or water chemistry. Although we did not see differences in 2016, we do not believe that breeding pools are selected randomly – we just did not measure the specific cue. For example, the snow had already melted before we arrived on site, so we were unable to determine if breeding pools had open water earlier than non-breeding pools. In addition, we did not differentiate pools where we have consistently observed successful breeding over the past eight years from pools where we have rarely seen breeding. We plan to improve our sampling design by beginning monitoring earlier in the season and pre-determining pools based on past breeding data in an attempt to measure differences between pools consistently used and pools consistently not used for breeding. Frogs used a diversity of pools in Carter Meadow for breeding including constant-leveled spring fed pools and shallow pools that dried early in the summer. The diversity of pools coupled with the groundwater-dominated hydrology may shed light on why the frog population persists when surrounding populations have been extirpated or are declining. Drought and Bd interact in complex ways to affect population structure of Cascades frogs (Pope et al. in prep.). While breeding in warm, shallow pools exposes larvae to desiccation under drought conditions; the warm water allows for rapid larval growth and may provide young frogs with a better chance of surviving with Bd when they metamorphose in warm water and air temperatures. In cold spring habitats, larvae are safe from desiccation but develop slowly and metamorphose later in the season into cooler air and water temperatures – conditions when the metamorphs tend to develop high loads of Bd (Hardy et al. 2015). By breeding in a range of pool conditions, the frogs may effectively be hedging their bets against two primary threats, drought and Bd.

DROUGHT EFFECTS ON RANGEWIDE POPULATION STATUS OF THE YOSEMITE TOAD AND SIERRA NEVADA YELLOW-LEGGED FROG

Field Methods

From 2002-2010, the USFS bioregional monitoring program (SNAMPH) surveyed all lakes, wet meadows, and a sample of stream reaches within 134 small watersheds (2-4 km² in size) for the Yosemite toad and 208 for the SNYLF. A subset of these (16 watersheds for the Yosemite toad and 26 watersheds for the SNYLF) were surveyed every year. Using this annually sampled set of sites, we identified lakes, wet meadows, and stream reaches that were surveyed multiple years from 2002-2010 and were occupied by any life stage of Yosemite toad or SNYLF at least one of the years. This resulted in a 2016 sample of 107 sites in 15 watersheds for the Yosemite toad on the Stanislaus, Toiyabe, Inyo, and Sierra National Forests (NF), and 60 sites in 7 watersheds for the SNYLF on the El Dorado, Stanislaus, Toiyabe, and Sierra NFs (Figure 18). Candidate Plumas and Tahoe sites were excluded because they were being surveyed by other projects in 2016.

In 2016, we conducted an early season and late season VES at each site between June and mid-September. Surveys were timed to maximize detection of tadpoles and depended on access due to snowmelt and risk of meadow desiccation. Watersheds within the Yosemite toad's range were surveyed earlier in the season, by mid-August, to reduce the risk of desiccation of ephemeral sites. Early and late visits allowed us to estimate the effect of later-season visits on detection of the species.

Two crew members independently surveyed all wadeable water at each site (lake, pond, wet meadow or selected stream reach) and recorded data on relative abundance of all life stages. Our methods were not designed to obtain precise abundance estimates; rather, the intent was to determine occupancy by life stage and to provide relative magnitudes of numbers of individuals.

Analysis

Results from the first monitoring cycle were reported at the watershed scale (Brown and Olsen 2013). Here we report results at both the watershed scale for comparison with the initial analysis and at the site scale (individual lake, meadow, or stream reach). We estimated the proportion of watersheds and sites with breeding activity (eggs, tadpoles, or metamorphs) and the proportion



Figure 18. Location of watersheds sampled during rangewide surveys of the Yosemite toad and SNYLF during 2016.

occupied by any life stage. Because we only sampled previously occupied sites, this analysis can estimate declines but not increases in occupancy. If no changes in occupancy had occurred for a given species since the last year of survey, we would have expected all sites to remain occupied in 2016.

We built detection histories for each species by tabulating the detection data for each species at each site for each observer and visit. Specifically, we built detection histories for two categories of life stages: 1) all life stages to assess species occurrence, and 2) tadpoles and metamorphs to assess evidence of breeding. These detection histories were used to estimate occupancy (ψ) and detection probability (p) using single-season single-species site occupancy models (MacKenzie et al. 2002). We analyzed each species separately for each group of life stages using a hierarchical modeling approach implemented in a Bayesian framework (MacKenzie et al. 2006, Kéry 2010). To account for the nested structure of the data (sites nested within watersheds), we included a random effect of watersheds on both the probability of detection and the probability of occupancy.

We included habitat type in the models to account for potential heterogeneity in occupancy. We used the categories meadow, lake, or stream for the Yosemite toad and the binary categories lake and meadow/stream for the SNYLF resulting in the following model for the Yosemite toad:

 $logit(\psi_i) = \alpha_{i(j)} + \beta_{Lake} * Lake_i + \beta_{Stream} * Stream_i$

and for the SNYLF:

 $logit(\psi_i) = \alpha_{i(j)} + \beta_{Lake} * Lake_i$

We modeled the effects of observer experience (experienced vs. new), Julian day (number of days elapsed since 1 January 2016), and time of day (early: < 1200, mid: 12:00 – 16:00, late: > 16:00) on the probability of detecting the species given their presence. The categories for the time of day factor were chosen to maintain a similar number of observations in each category and to model potential nonlinear relationships with time.

Bayesian models require specifying expected values of the parameters being estimated. Here, we used vague prior distributions for all parameters meaning we assumed little prior knowledge (Kéry 2010, Link and Barker 2010). Specifically, we used uniform(-10, 10) priors on all β parameters, uniform(0, 70) priors on all standard deviation parameters, and a normal distribution with mean 0 and variance 100 on the hyperparameter of the random intercepts.

We used Markov chain Monte Carlo (MCMC) to estimate the posterior distribution of the parameters using five chains (Link and Barker 2010, Gelman et al. 2014). All analyses were implemented in JAGS 4.1.0 (Lunn et al. 2013) within R with the R2jags and coda packages (Plummer et al. 2006, Su and Yajima 2015, R Core Team 2016). We reported means and 95% credible intervals (95% CRI) for each parameter of interest. We computed predicted occupancy for average sites and each watershed. We also used the sum of the latent occupancy state (*z*) to estimate the number of occupied sites in each watershed.

Results

In 2016, evidence of Yosemite toad breeding (eggs, tadpoles, or metamorphs) was found in an estimated 46 (95% CRI: 44-49) of the 107 sites surveyed with prior occupancy of any life stage. Evidence of breeding was found in an estimated fourteen of the fifteen watersheds (95% CRI: 14-15) (Figure 19A). Yosemite toads of any life stage were found in an estimated 58 (95% CRI: 57-61)

of the 107 sites surveyed with prior occupancy of any life stage, and in all 15 watersheds surveyed (Figure 19B). The probability of detecting tadpoles or metamorphs was affected by Julian day, observer experience, and time of survey, whereas the probability of detecting any life stage was only influenced by Julian day (Table 2). Probability of detection decreased over the summer (Figure 20). Probability of detection remained over 0.8 until mid-August when it declined sharply.



Figure 19. Probability of occupancy of (A) breeding of Yosemite toad (*Anaxyrus canorus*), determined from detection of tadpoles and metamorphs, and (B) any life stage at California sites in each watershed sampled in 2016. Note that only habitat types occurring in sampled sites of each watershed are shown.

Figure 19 shows estimated site occupancy by habitat type for each of the watersheds surveyed. If all sites remained occupied in 2016, then the probability of occupancy would be 1. Occupancy was relatively consistent among watersheds for the different habitat types for both breeding and any life stages. Streams were less likely to remain occupied, though fewer streams were sampled. Brown et al. (2012) found that some sites tended to be consistently occupied across years whereas others were more sporadically occupied. To examine whether this may explain the low site occupancy rates, we compared occupancy in 2016 to the number of years of prior occupancy from 2002-2010. For both breeding and any life stage, sites that had been consistently occupied more years during 2002-2010 were more likely to be occupied in 2016 (Figure 21A, Breeding: t = -9.65, df = 105, p = <.0001, Any stage: t = -8.59, df = 105, p = <.0001).

Evidence of SNYLF breeding was found in an estimated 24 (95% CRI: 20-32) of the 60 sites surveyed with prior occupancy of any life stage. Breeding was found in an estimated five of the seven watersheds (95% CRI: 4-7) (Figure 22A). Frogs of any stage were found in 42 (95% CRI: 36-46) of the 60 sites surveyed with prior occupancy including an estimated five of the seven watersheds

Data	Parameter type	Parameter	Posterior mean	95% credible interval
occurrence (all life stages)	occupancy	Lake	0.18	[-0.78, 1.16]
		Stream	-0.86	[-2.32, 0.53]
		σ_{psi} watershed	0.44	[0.02, 1.26]
	detection probability	Julian day	-0.76	[-1.20, -0.34]
		Observer.new	-0.61	[-1.26, 0.02]
		Time.mid	-0.57	[-1.34, 0.18]
		Time.late	-0.76	[-1.75, 0.22]
		$\sigma_{\text{psi watershed}}$	0.56	[0.05, 1.31]
	occupancy	Lake	-0.18	[-1.14, 0.78]
evidence of breeding (tadpoles, metamorphs)		Stream	-2.79	[-5.96, -0.67]
		σ_{psi} watershed	0.39	[0.01, 1.21]
	detection probability	Julian day	-0.96	[-1.46, -0.49]
		Observer.new	-0.77	[-1.53, -0.01]
		Time.mid	-0.86	[-1.82, 0.04]
		Time.late	-1.62	[-2.84, -0.46]
		$\sigma_{\text{psi watershed}}$	0.47	[0.03, 1.28]

Table 2. Posterior means and precision of slope parameters on probabilities of occupancy and detection of Yosemite toad (*Anaxyrus canorus*) in 2016 in California at 107 sites known to be occupied in previous years. $\sigma_{psi watershed}$ is the variation explained by watershed.

Predictions ± 95% credible interval



Figure 20. Detection probability of Yosemite toad breeding (*Anaxyrus canorus*) decreasing with Julian day of the surveys conducted in 2016.



Figure 21. Occupancy in 2016 relative to number of years of prior occupancy from 2002-2016 for (A) Yosemite toad and (B) SNYLF.

surveyed (95% CRI: 5-7, Figure 22B). The detection probability of SNYLF breeding or any stage did not vary with any of the variables we considered (Table 3). The probability of detecting evidence of SNYLF breeding was 0.46 (95% CRI: 0, 1) and any stage of SNYLF was 0.77 (95% CRI: 0.10, 0.99). The 95% credible intervals for these estimates were large due to the small sample sizes.

SNYLF showed variation in occupancy among watersheds (Figure 22). Watersheds with large populations (e.g., 28536, 28426) had higher probability of occupancy, whereas occupancy was much lower in watersheds where we only found a few frogs in a few years (e.g., 27682, 24010). The probability of finding adults or subadults was higher than breeding. Sites that were more consistently occupied during the period 2002-2010 were more likely to be occupied in 2016 (Figure 21B, Breeding: t = -7.63, df = 58, p = <.0001, Any stage: t = -5.67, df = 58, p = <.0001).

Data	Parameter type	Parameter	Posterior mean	95% credible interval
occurrence (all life stages)	occupancy	Lake	1.21	[-0.99, 3.79]
		$\sigma_{\sf psi}$ watershed	2.60	[0.12, 10.38]
	detection probability	Julian day	-0.10	[-0.48, 0.26]
		Observer.new	-0.62	[-1.41, 0.14]
		Time.mid	0.26	[-0.87, 1.38]
		Time.late	-0.91	[-1.99, 0.14]
		$\sigma_{p \ watershed}$	5.36	[1.13, 18.40]
evidence of breeding (tadpoles, metamorphs)	occupancy	Lake	0.40	[-1.62, 2.59]
		$\sigma_{\text{psi watershed}}$	3.25	[0.25, 13.75]
	detection probability	Julian day	-0.38	[-0.96, 0.16]
		Observer.new	-0.16	[-1.27, 0.95]
		Time.mid	2.00	[-0.22, 4.34]
		Time.late	1.22	[-0.94, 3.30]
		σ_p watershed	9.02	[0.77, 39.86]

Table 3. Posterior means and precision of parameters on probabilities of occupancy and detection of Mountain yellow-legged frog (*Rana sierrae*) in 2016 in California at 107 sites known to be occupied in previous years. $\sigma_{\text{nsi watershed}}$ is the variation explained by watershed.

Discussion

The results from our 2016 surveys did not indicate a strong effect of the drought on Yosemite toad and SNYLF occupancy. Occupancy at the watershed scale was high, particularly for the Yosemite toad, and we found both species in the majority of sites that were consistently occupied in the past.

SNAMPH, the USFS bioregional monitoring program, reported occupancy results at the watershed scale. They chose this approach because studies suggest that larger scales may more effectively distinguish regional trends from local population fluctuations (Hecnar and M'Closkey 1997, see Brown and Olsen 2013 for more discussion). Further, metapopulation theory often is applied to amphibian conservation, suggesting that the loss or decline in numbers of animals in one site may not necessarily be cause for concern, whereas the loss of animals in multiple sites within an area may reflect a genuine decline. Thus, to examine the effects of the drought on the Yosemite toad and SNYLF, we evaluated occupancy at both watershed and site scales; this combination provides the most insights into a species status.

The high proportion of occupied watersheds in 2016 suggests that there was no widespread decline in the Yosemite toad. The one watershed where evidence of Yosemite toad reproduction was not found was surveyed relatively late in the season and, after accounting for probability of detection, our model suggests it had about 0.4 probability of being occupied. Occupancy was lower at the site scale in 2016, but this is similar to what was found in previous years where, in the same suite of



Figure 22. Probability of occupancy of (A) SNYLF (*Rana sierrae*) breeding, determined from detection of tadpoles and metamorphs, and (B) any life stage at California sites in each watershed sampled in 2016. Note that only habitat types occurring in sampled sites of each watershed are shown. Note that the « other » habitat type includes meadows and streams.

watersheds, only 30% of the sites were consistently occupied every year (Brown et al. 2012). Our 2016 results also support the finding of Brown et al. (2012) that one or two sites in each watershed tended to be occupied every year, while others were occupied more sporadically. The sites that were consistently occupied in previous years remained occupied in 2016, whereas the sites that were not occupied in 2016 were occupied more sporadically in previous years.

In 2016, we found SNYLF in the watersheds where we consistently found them in prior years, but not in the watersheds where only a few animals had been found in only a few years. Whether the latter areas are still occupied is unknown, but it is possible that frogs were present in 2016 but we did not find them in part due to the small populations. Similar to the Yosemite toad, Brown et al. (unpublished data) found that SNYLF tended to occupy some sites consistently and others more sporadically, but the sample size for evaluation was small. The SNYLF has a multi-year tadpole stage, so presumably, evidence of breeding should be consistently observed from year to year unless mass mortality occurs. Most of the sites occupied by breeding in 2016 were consistently occupied during the previous survey period, whereas most of the sites with no signs of breeding in 2016 also had no signs of breeding in most or all of the prior years of survey. This pattern was similar for frogs of any life stage, though more of the sites with no detections in 2016 had been occupied in prior years. SNYLF adults move among sites during the season, many of which may not be suitable for breeding (Matthews and Preisler 2010). It is important to note that occupancy only measures the presence of a species and is not necessarily indicative of the resilience of single populations. Many populations of both Yosemite toad and SNYLF are very small and thus may be vulnerable to extinction from stochatic or other factors. Whether abundances of these species declined during the drought is not known. The amount and persistence of Yosemite toad breeding habitat in some meadows was greatly reduced during the drought years. In addition, behavioral changes were observed in some Yosemite toad populations to the point that no breeding occurred in some years (C. Brown and S. Barnes unpublished data). The long-term effect of these drought-related patterns on persistence remains to be determined.

The Yosemite toad and SNYLF have life strategies that enable them to persist in the high elevation, unpredictable environments they inhabit in the Sierra Nevada. They are long-lived, which may enable populations to persist even though reproduction efforts may fail in unfavorable years. In our 11 year capture-mark-recapture monitoring, our oldest documented Yosemite toad adult is at least 13 years assuming a 3 year subadult stage. Matthews and Miaud (2007) documented mountain yellow-legged frog taxa up to 14 years of age. Thus, for both species, populations would have persisted through the four-year drought if adults survived. The highly aquatic SNYLF adults may be more susceptible to the drought if their habitats dry out than Yosemite toad adults who use terrestrial environments. On the other hand, SNYLF tadpoles using deeper perennial waters may be buffered from the drought effects compared with Yosemite toads who breed in very shallow ephemeral waters. Several Yosemite toad breeding meadows did not have surface water habitat available for breeding in 2013-2015. SNYLF that inhabit smaller, shallower sites may be particularly vulnerable to habitat desiccation. There is likely a limit to the duration a population can survive a prolonged drought governed by population size, degree habitats desiccate, and severity of drought.

During the drought years, the growing season was longer than usual, which may have benefitted the species. Our general observations were that during the drought years, Yosemite toad metamorphs, when they survived, were larger and fatter than usual toward the end of the summer. Adult toads and SNYLF may have benefitted from the long growing season as well.

Detection probabilities were generally high, were similar to those found in previous surveys, and made sense given the life histories of the two species. Detection probabilities for the two taxa were estimated at the watershed scale for the SNAMPH surveys conducted from 2002-2009 (Brown et al. 2012, Brown et al. 2014). These watershed scale estimates were calculated from single visits per season compiled across years. This confounds several components of detection, the probability that individuals are available for detection and the probability of finding individuals given their availability. The 2016 surveys were explicitly designed to account for these components. The probability of detection for the Yosemite toad from 2016 surveys was very similar to that found in the SNAMPH surveys. Detection of tadpoles was ≥ 0.8 if surveys are conducted early enough in the season (e.g., prior to mid-August). The probability of detection for SNYLF in 2016 also was comparable to the SNAMPH survey results.

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LITERATURE CITED

- Brown, C., and A.R. Olsen. 2013. Bioregional monitoring design and occupancy estimation for two Sierra Nevadan amphibian taxa. Freshwater Science. 32:675-691.
- Brown, C., L. Wilkinson, and K. Kiehl. 2014. Comparing the Status of two Sympatric Amphibians in the Sierra Nevada, California: Insights on Ecological Risk and Monitoring Common Species. Journal of Herpetology, 48:74-83.
- Brown, C.; K. Kiehl, and L. Wilkinson. 2012. Advantages of long-term, multi-scale monitoring: Assessing the current status of the Yosemite toad (Anaxyrus [Bufo] canorus) in the Sierra Nevada, California, USA. Herpetological Conservation and Biology. 7: 115-131.
- Crump, M.L., and N.J. Scott. 1994. Visual encounter surveys. Pp. 84–92 In Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Heyer W.R., M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster. (Eds.). Smithsonian Institution Press, Washington, D.C., USA.
- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2014. Bayesian data analysis, 3rd edition. CRC Press, Boca Raton, FL, USA.
- Hardy, B. M., K. L. Pope, J. Piovia-Scott, R. N. Brown & J. E. Foley (2015) Itraconazole treatment reduces Batrachochytrium dendrobatidis prevalence and increases overwinter field survival in juvenile Cascades frogs. *Diseases of Aquatic Organisms*, 112, 243-250.
- 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). Ann Arbor, MI: University of Michigan. Ph.D. dissertation. 394 p.
- Karlstrom, E.L. 1962. The toad genus Bufo in the Sierra Nevada of California: ecological and systematic relationships. University of California Publications in Zoology. 62: 1–104.
- Kéry, M. 2010. Introduction to WinBUGS for ecologists: a Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, New York, USA.
- Link, W. A., and R. J. Barker. 2010. Bayesian inference with ecological applications. Academic Press, Boston.
- Lunn, D., C. Jackson, N. Best, A. Thomas, and D. Spiegelhalter. 2013. The BUGS book: a practical introduction to Bayesian analysis. CRC Press, Boca Raton, FL, USA.

- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, New York.
- Matthews, K. R., and C. Miaud. 2007. A skeletochronological study of the longevity and age structure of the mountain yellow-legged frog, *Rana muscosa*, in the Sierra Nevada. Copeia, 4:984-991.
- Olson, D.H., W.P. Leonard, and R.B. Bury (Eds.). 1997. Sampling Amphibians in Lentic Habitats. Northwest Fauna 4. Society for Northwestern Vertebrate Biology, Olympia, Washington, USA.
- Plummer, M., Best, N., Cowles, K., and K. Vines. 2006. CODA: Convergence diagnosis and output analysis for MCMC, R News 6:7-11.
- <u>R Core Team (2016).</u> R: A language and environment for statistical computing. R Foundation for <u>Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.</u>
- Su, Y.-S., and M. Yajima. 2015. R2jags: Using R to run JAGS. R package version 0.5-7. https://CRAN.R-project.org/package=R2jags.
- U.S. Fish and Wildlife Service [USFWS]. 2014. Endangered and Threatened Wildlife and Plants; Endangered Species Status for Sierra Nevada Yellow-Legged Frog and Northern Distinct Population Segment of the Mountain Yellow-Legged Frog, and Threatened Species Status for Yosemite Toad; Final Rule. Federal Register. 79:24256-24310. [29 April].