Fine-Scale Habitat Characteristics Related to Occupancy of the Yosemite Toad, *Anaxyrus canorus*

Christina T. Liang\(^1\), Robert L. Grasso\(^1\), Julie J. Nelson-Paul\(^1\), Kim E. Vincent\(^1\), and Amy J. Lind\(^1\)

Fine-scale habitat information can provide insight into species occupancy and persistence that is not apparent at the landscape-scale. Such information is particularly important for rare species that are experiencing population declines, such as the threatened Yosemite Toad (*Anaxyrus canorus*). Our study examined differences in physical characteristics of occupied and unoccupied toad breeding pools within meadows, and then used a logistic regression model to evaluate if occupancy was related to the physical microhabitat variables. We found that occupied pools on average were deeper by 0.7 cm, warmer by 3°C, and had greater surface water along the short axis of the pool. Mean water depth, mean water temperature, the amount of surface water in the pools, mean detritus depth, and mean vegetation height were significant predictors of toad occupancy. Despite variation in larger-scale environmental conditions such as yearly winter snow cover and precipitation, occupancy was not related to individual years and microhabitat requirements for toad occupancy appear to be relatively constant. Pools were very shallow water bodies (mean depth 4.35 cm for occupied pools), and differences in physical microhabitat variables for suitable breeding sites were small but significant. This underscores the importance of fine-scale habitat information for breeding and reproduction of *A. canorus*, and for species persistence and management.

Occupancy models typically cover the entire species range and provide valuable information on overall species distribution. While landscape-scale processes are important predictors of amphibian occupancy for some species (Scherer et al., 2012), range-wide models do not provide information on the finer-scale factors related to species presence. Fine-scale information is of particular interest for rare species, where variables at the microhabitat scale can help explain the specific habitat requirements for species persistence. Knowledge of rare species’ microhabitat requirements can then help wildlife managers carefully consider suitable habitat for conservation efforts and also for potential re-introductions. One such species for which this information is needed is the Yosemite Toad (*Anaxyrus canorus*), a high-elevation amphibian species endemic to the Sierra Nevada mountain range in California. The historical range for *A. canorus* is approximately Ebbetts Pass in the north (Alpine County) to the Kings River in the south (Fresno County), at 1,950 m to above 3,400 m in elevation (Jennings and Hayes, 1994). Populations throughout the historical range have declined for unknown reasons, and the species is listed as federally threatened under the U.S. Endangered Species Act (USFWS, 2014).

*Anaxyrus canorus* is associated primarily with montane wet meadows that are used for breeding and larval development, although adults also are found in upland terrestrial habitats (Morton and Pereyra, 2010; Liang, 2013). Breeding occurs in various wetted areas from shallow standing water to small depressions, ponds, slow-flowing streams, and edges of lakes (Karlstrom and Livezey, 1955; Karlstrom, 1962; Kagarise Sherman, 1980). Males arrive first at breeding areas and spend more time at the sites than females. Individual females do not breed every year (Kagarise Sherman and Morton, 1993). Egg deposition and larval development typically occur in shallow, ephemeral, and warm water microhabitats; metamorphosis typically occurs within six to eight weeks of egg deposition (Mullally, 1953; Karlstrom, 1962; Kagarise Sherman, 1980; Kagarise Sherman and Morton, 1984). Interannual climate variability likely plays a strong role in breeding success. Shallow microhabitats are often subjected to freezing nighttime water temperatures, which can compromise egg masses. During years of low snowpack or precipitation, aquatic habitats can dry completely before larvae can complete metamorphosis, which results in tadpole mortality (Kagarise Sherman, 1980; Kagarise Sherman and Morton, 1984). The survival of eggs and tadpoles to metamorphosis thus likely depends on surface water persistence and water temperature in pools (Kagarise Sherman and Morton, 1993).

Range-wide occupancy models for *A. canorus* have used the meadow as the unit of occupancy in order to evaluate predictor variables at the landscape scale (Liang et al., 2010; Liang and Stohlgren, 2011; Berlow et al., 2013). Within occupied meadows, however, there is variability in the occupancy of microhabitats (Brown et al., 2012) and toads often use only a small subset of available microhabitats within meadows for breeding (Karlstrom, 1962; Sadinski, 2004). This appears to be due to toads selecting particular microhabitats rather than a function of the number of breeding toads per meadow (pers. obs.). In order to gain a better understanding of microhabitat selection by *A. canorus* at the fine-scale pool level, we examined differences in pool physical characteristics for occupied and unoccupied pools. We then used a logistic regression model to evaluate if occupancy is related to pool microhabitat variables. Our working hypothesis was that pools occupied by *A. canorus* would have relatively higher water temperatures and greater water volumes, and that these microhabitat variables are significant for toad occupancy.

**Materials and Methods**

From 2005 through 2010, we collected data from ten meadows in the Sierra National Forest and seven meadows in the Stanislaus National Forest. We collected data from an

---

\(^1\) USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Dr., Davis, California 95618; Email: (CTL) christinaliang@fs.fed.us; (RLG) rob_grasso@nps.gov; (JJNP) julsjpaul@gmail.com; (KEV) kimevincent@gmail.com; and (AJL) alind@fs.fed.us. Send reprint requests to CTL.


© 2017 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CH-15-290 Published online: 13 April 2017
additional two meadows in Yosemite National Park from 2007 through 2010. The meadows are located at approximately 2,120 m to 2,680 m in elevation throughout the historical range of *A. canorus* (Fig. 1). Meadows range in size from 0.7 ha to 23.3 ha.

We surveyed the meadows in three sampling periods every year: (1) late spring for adult toads and eggs, typically in May and June, (2) early to mid-summer for tadpoles, typically in May through July, and (3) late summer for newly metamorphosed individuals, typically in August and September. Visits to each meadow were timed to coincide with the developmental phases of toads, from egg to tadpole to metamorphosed young-of-the-year. Lower elevation meadows were visited before higher elevation meadows, as lower elevations typically had earlier snowmelt and breeding normally occurred at these locations first. To the extent feasible, we timed our sampling of tadpoles so that they were at roughly the same developmental stage each year, thus reducing variability for estimates of change over time.

The majority of meadows were surveyed at least two times during both the late spring and late summer sampling periods and at least one time during the early to mid-summer sampling period each year. Perennially dry and/or steeply sloped portions in meadows were excluded from the survey area.

At the start of the study, we intensively surveyed each meadow to identify pools that contained eggs and/or tadpoles of *A. canorus*. Pools occupied during this first survey were designated as “Present” pools. To compare with Present pools, we selected up to three pools per meadow without eggs and/or tadpoles at the start of the study and designated these as “Potential” pools. Potential pools were selected for potential suitability for breeding of *A. canorus*, based on visual assessment of microhabitat characteristics of the pool including shallow water depth and amount of water in pool. We placed an identified marker stake in the approximate center of every designated pool (Present and Potential) and recorded the GPS location of the stake using a Garmin eTrex Legend GPS (accuracy ±3 m with 95% confidence). The marker stake was used as a reference point for consistent measurements around a central point that best characterized the pool habitat, both within and among years. If an unmarked and undesignated pool was occupied in subsequent surveys, it was added to the study as a Present pool.

We surveyed 143 pools in the 19 meadows at least once during our study period. Occupancy, defined as having eggs or tadpoles of *A. canorus*, varied over the study period for the designated pools; not all Present pools were occupied and not all Potential pools were unoccupied for every year of the study. For pools that were surveyed in two or more years (128 pools), 27.3% were never occupied and 21.9% were always occupied. The remaining 50.8% of pools were occupied at least once. The number of occupied pools in each meadow each year ranged from one to 11, and generally was related to the size of the meadow. Larger meadows typically had a larger number of occupied pools every year. Probability of imperfect detection was reduced through the repeated surveys of the same meadow each year.

**Pool variables.**—During the early to mid-summer sampling period, we recorded microhabitat variables for every designated pool. We set up three transects through each pool using meter tapes, and transects were centered on the marker stake in the pool. If tadpoles were not near the stake, transects were centered on the tadpoles. This occurred rarely and the length of transects still ensured that the overall pool was characterized, and not only the locations with tadpoles. We placed the first transect (T1) parallel with the long axis of the pool, i.e., along the longest wetted area. T1 was 5 m long in 2005 and 10 m long in 2006–2010. We placed a 5 m long transect (T2) perpendicular to T1, and a second 5 m long transect (T3) at a 45-degree angle to T1 and T2 in all years.

Along each of the three transects, we recorded the following data at every meter point starting at 0 m: water temperature, water depth, detritus depth, and live vegetation height. Water temperature was recorded in degrees Celsius using a pocket case thermometer (accuracy 0.5°C). Water depth in cm was measured using clear plastic rulers (accuracy 1 mm) as the depth of the water, including loose detritus. Detritus depth in cm was measured as the portion of water depth which contained loose, flocculent material. Live vegetation height in cm was measured from the base of the vegetation to the straight-line tip using clear plastic rulers or meter tape (accuracy 2 mm) if vegetation was over 30 cm.

For each transect, we recorded overall water condition through an estimate of the percentage of the transect that had standing surface water or was dry. We also visually estimated the percent canopy closure (ranging from 0=open to 100=closed) for each transect.

**T-tests for pool variables.**—We used two-sample t-tests assuming equal variances to compare mean microhabitat values for occupied versus unoccupied pools from all years of the study. Occupied pools were defined as having eggs or tadpoles of *A. canorus* during any of the survey periods in a given single year, although the microhabitat variables were recorded during the early to mid-summer sampling period in that year. Mean values for the entire pool were calculated for detritus depth, live vegetation height, water depth, water temperature, and overall water condition using the transect data. Missing data points were deleted from the calculation of the mean values.

**Logistic regression.**—We analyzed pool occupancy in relation to pool microhabitat variables by fitting a global generalized linear mixed-effects model (GLMM) using the glmer function in the *lme4* package in R (Bates et al., 2015; R version 3.2.1, R Core Team, 2015). We then employed a model averaging method to generate a summary model from subset models based on the corrected Akaike information criterion (AICc; Grueber et al., 2011), using the dredge and model.avg functions in the *MuMIn* package (Barton, 2015). We used a cutoff of 2AICc to generate the submodel set that was averaged in the summary model (Burnham and Anderson, 2002). Model averaging accounts for uncertainty in model selection and provides robust parameter estimates, particularly when there is no single best model for the data and models have small differences in their fit, based on an information criterion (Grueber et al., 2011).

We used a logistic regression for our GLMM with pool occupancy each year as the dependent variable, and pool and meadow as nested random effects. The nesting accounts for the hierarchical structure of pools within meadows, and the random effects account for repeated measurements on the experimental units (pools). Occupied pools were defined as for the t-test analysis.

Predictor variables in the global model included the mean values for the transect data collected at each meter point in the three transects (i.e., water depth, detritus depth, water
temperature, and live vegetation height), with the mean value representing the entire pool (same mean values as for the t-tests). Other predictor variables in the global model were percent standing surface water, percent dry ground, and percent canopy closure for each of the three transects in the pool. We included year as a categorical predictor value and set the contrasts to sum to zero. To identify any nonlinear forms of the predictors, we fit a generalized additive mixed
model (GAMM) to the data using function gamm4 in the gamm4 package (Wood and Scheipl, 2014).

RESULTS

T-tests for pool variables.—There were significant differences in the microhabitat variables measured during the early to mid-summer sampling period in occupied pools compared to unoccupied pools, based on two-sample two-tailed t-tests assuming equal variances. Occupied pools had significantly greater mean water depth ($P = 0.001$), mean water temperature ($P < 0.001$), and percent surface water in T2 ($P < 0.001$; Table 1). Occupied pools had lower mean vegetation height, although the difference was not significant ($P = 0.079$). Detritus depth did not vary between pools ($P = 0.383$). Microhabitat variables showed variability between years (Fig. 2).

Logistic regression.—For the logistic regression analysis, we excluded pools with missing predictor values. The resultant dataset includes 589 observations from 139 pools in the 19 study meadows through all years of the study.

Cross correlations were examined for all variables to test multicollinearity. We identified one set of highly correlated variables (Pearson’s correlation coefficient $\geq 0.80$), which was the percent standing water in T2 and T3. We included the T2 variable and not the T3 variable in the regression, based on likely contribution to potential distribution and ecological relevance for A. canorus. We did not transform any variables for the regression analysis because model fit did not improve by including smoothing terms for nonlinearity in the predictors, based on the GAMM analysis.

The global mixed-effects logistic regression model is as follows:

$$\logit[\theta(\text{Occupied} = 1)] = \beta_0 + \beta_1(\text{Year}) + \beta_2(\text{Mean Detritus Depth}) + \beta_3(\text{Mean Vegetation Height}) + \beta_4(\text{Mean Water Depth}) + \beta_5(\text{Mean Water Temperature}) + \beta_6(\text{T1%Surface Water}) + \beta_7(\text{T1%Dry Ground}) + \beta_8(\text{T1%Canopy Cover}) + \beta_9(\text{T2%Surface Water}) + \beta_{10}(\text{T2%Dry Ground}) + \beta_{11}(\text{T2%Canopy Cover}) + \beta_{12}(\text{T3%Dry Ground}) + \beta_{13}(\text{T3%Canopy Cover}) + (1|\text{Meadow}) + (1|\text{Pool}) + e_i$$

Table 1. Mean values for microhabitat variables in occupied and unoccupied pools from 2005–2010. *significant at $\alpha = 0.05$.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Occupied pools</th>
<th>Unoccupied pools</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>$n$</td>
<td>Mean</td>
</tr>
<tr>
<td>Detritus depth (cm)</td>
<td>1.62</td>
<td>303</td>
<td>1.69</td>
</tr>
<tr>
<td>Vegetation height (cm)</td>
<td>13.20</td>
<td>301</td>
<td>14.16</td>
</tr>
<tr>
<td>Water depth (cm)</td>
<td>4.35</td>
<td>307</td>
<td>3.65</td>
</tr>
<tr>
<td>Water temperature (degrees C)</td>
<td>24.82</td>
<td>307</td>
<td>21.75</td>
</tr>
<tr>
<td>T2 surface water (%)</td>
<td>60.57</td>
<td>308</td>
<td>40.07</td>
</tr>
</tbody>
</table>

Fig. 2. Mean values and SE bars for pool microhabitat variables in unoccupied and occupied pools from 2005–2010. Differences for all years combined are significant for mean water temperature, mean water depth, and percent surface water in T2 (two-tailed t-test; $P < 0.05$ for all).
where $\theta$(Occupied=1) is the probability of occupancy, $\beta_0$ is the intercept, the $\beta$s are the fixed effects regression coefficients, and $\epsilon_i$ is the model residual term. (1|Meadow) and (1|Pool) are the random effects, with separate random intercepts for each pool nested within meadow.

The model-fitting process produced a set of 17 models with $\Delta$AICc values less than two, and this set of models was used to produce average parameter estimates and 95% confidence intervals. The summary model showed that mean water depth, mean water temperature, percent surface water in T2, mean detritus depth, and mean vegetation height were all significant predictors of occupancy ($P < 0.050$; Table 2). Parameter estimates showed that occupancy was positively related to the mean water depth, mean water temperature, and the percent surface water in T2; occupancy was negatively related to the mean detritus depth and mean vegetation height. The relative importance of each predictor in the summary model is the sum of Akaike weights over all models including the explanatory variable (Barton, 2015), and the five significant predictor variables also had the highest relative importance (Table 2). The year variable did not appear in any of the top 2AICc models and so was not included in the summary model.

For continuous variables, the odds ratio is the change in odds for a unit increase in the predictor variable, holding all other variables constant. Odds ratio values above one are the percentage increase in odds of occupancy for a unit increase in predictor value. Odds ratio values below one are the percentage decrease in odds of occupancy for a unit increase in predictor value. Mean water depth in our model had the largest overall odds ratio, and we would expect a 46.7% increase in occupancy odds for a one cm increase in water depth, if all other variables were held at a fixed value. Mean detritus depth had the largest odds ratio less than one, and we would expect a 42.0% decrease in occupancy odds for a one cm increase in detritus depth, if all other variables were held at a fixed value (Table 2).

## DISCUSSION

Patterns of occupancy for *A. canorus* emerge at the pool microhabitat scale and provide insight into the specific habitat requirements for this threatened species. As hypothesized, surface water properties in the microhabitat were strongly related to toad occupancy of pools. This is not surprising given that eggs and tadpoles of *A. canorus* require environmental conditions that are conducive to rapid metamorphosis. Our study verified that the significant predictors of occupancy by *A. canorus* are mean water depth, mean water temperature, and the amount of surface water in the microhabitat. On average, occupied pools were deeper by 0.7 cm, warmer by 3°C, and had 50% more surface water along the short axis of the pool. These conditions likely contribute to quicker developmental times in the shallow-water ephemeral habitats which are available only during a short period in the spring and summer. Even though differences in some of these environmental variables were not large, they were significant for occupancy and underscore the importance of fine-scale microhabitat information for breeding and reproduction of *A. canorus*.

Our results contrast with a companion study by Roche et al. (2012), who investigated two occupied and two unoccupied pools each in nine meadows (36 pools total) in 2006–2008. Across years, they found that *A. canorus* occupied warmer but shallower pools. Our study found that *A. canorus* occupied deeper pools; however, we analyzed occupancy each year rather than across years. Individual year analysis provides information on why the same pool might be occupied in some years but not in others. The selection of unoccupied pools for comparative purposes in a study also can affect the results. While *A. canorus* may use pools that are shallower than other pools in the meadow overall, they appear to breed in pools that are deeper in a given year relative to other years. Breeding pools are very shallow water bodies (mean depth 4.35 cm for occupied pools), and differences in depth between pools that are occupied and unoccupied each year are small but significant.

Detritus and vegetation in the microhabitat also were related to occupancy by *A. canorus*; however, the differences in occupied and unoccupied pools were not significant. On average, detritus depth in occupied pools was smaller than in unoccupied pools but by less than 1 mm. Vegetation in occupied pools was shorter by almost 1 cm than in unoccupied pools. The mechanisms underlying these relationships are not known, and may relate to other physical or chemical resources available in the pool. Tadpoles of *A. canorus* often are found within the detritus layer (pers. obs.), which is a food source and also provides visual protection from predators. However, detritus depth may affect water depth and temperature or other chemical properties of the

---

### Table 2. Summary results after model averaging based on the top 2AICc of models. Results show effects of each parameter on pool occupancy by Yosemite Toad. *significant at $\alpha = 0.05$. Year variable not included in top 2AICc of models.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate (std. error)</th>
<th>95% Confidence interval</th>
<th>P value</th>
<th>Odds ratio</th>
<th>Relative importance</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>−3.84 (0.87)</td>
<td>−5.56, −2.13</td>
<td>&lt;0.000*</td>
<td>0.580</td>
<td>1.00</td>
</tr>
<tr>
<td>Detritus depth, mean (cm)</td>
<td>−0.55 (0.20)</td>
<td>−0.94, −0.15</td>
<td>0.006*</td>
<td>0.927</td>
<td>1.00</td>
</tr>
<tr>
<td>Vegetation height, mean (cm)</td>
<td>−0.08 (0.03)</td>
<td>−0.14, −0.02</td>
<td>0.012*</td>
<td>0.969</td>
<td>0.05</td>
</tr>
<tr>
<td>Water depth, mean (cm)</td>
<td>0.38 (0.10)</td>
<td>0.18, 0.58</td>
<td>&lt;0.000*</td>
<td>1.467</td>
<td>1.00</td>
</tr>
<tr>
<td>Water temp, mean (°C)</td>
<td>0.11 (0.02)</td>
<td>0.06, 0.15</td>
<td>&lt;0.000*</td>
<td>1.113</td>
<td>1.00</td>
</tr>
<tr>
<td>T1 surface water (%)</td>
<td>0.01 (0.01)</td>
<td>−0.01, 0.02</td>
<td>0.298</td>
<td>1.008</td>
<td>0.20</td>
</tr>
<tr>
<td>T1 dry ground (%)</td>
<td>−0.03 (0.04)</td>
<td>−0.10, 0.04</td>
<td>0.384</td>
<td>0.965</td>
<td>0.66</td>
</tr>
<tr>
<td>T1 canopy cover (%)</td>
<td>−0.04 (0.02)</td>
<td>−0.08, 0.01</td>
<td>0.107</td>
<td>0.956</td>
<td>0.66</td>
</tr>
<tr>
<td>T2 surface water (%)</td>
<td>0.03 (0.01)</td>
<td>0.01, 0.04</td>
<td>&lt;0.000*</td>
<td>1.027</td>
<td>1.00</td>
</tr>
<tr>
<td>T2 dry ground (%)</td>
<td>0.03 (0.02)</td>
<td>−0.02, 0.07</td>
<td>0.253</td>
<td>1.026</td>
<td>0.17</td>
</tr>
<tr>
<td>T2 canopy cover (%)</td>
<td>−0.02 (0.03)</td>
<td>−0.08, 0.04</td>
<td>0.485</td>
<td>0.980</td>
<td>0.13</td>
</tr>
<tr>
<td>T3 dry ground (%)</td>
<td>0.04 (0.03)</td>
<td>−0.02, 0.09</td>
<td>0.176</td>
<td>1.039</td>
<td>0.40</td>
</tr>
<tr>
<td>T3 canopy cover (%)</td>
<td>−0.06 (0.05)</td>
<td>−0.15, 0.04</td>
<td>0.234</td>
<td>0.946</td>
<td>0.31</td>
</tr>
</tbody>
</table>
pool. Vegetation was in early stages of growth during the early to mid-summer sampling period but still was a source of shade. Through shading, vegetation might affect the light, thermal, and primary production in the pool environment similar to the effects of forest canopy. Studies of open and closed forest canopy over ponds have shown that open canopy ponds have higher average water temperatures and contain more amphibian species than closed canopy ponds (Freidenburg and Skelly, 2004; Skelly et al., 2014). In our study, reduced shading from lower vegetation in occupied pools might also lead to higher water temperatures and increased food resources, which are beneficial for tadpole development. Although canopy cover was not a significant predictor of occupancy by *A. canorus*, there were negative relationships between canopy cover in all transects and toad occupancy. Canopy cover may not be significant in our study because the meadows do not contain much cover in general.

Pools can change occupancy status from year to year, likely due to yearly environmental conditions such as winter snow cover and precipitation. Microhabitat conditions in pools are affected by ambient conditions, and pools may not be suitable for occupancy depending on these larger-scale conditions. During our study period, year 2005 had the highest precipitation during our study in the first six months of the water year (1 October 2004–31 March 2005) and had the highest percentage of occupancy by *A. canorus*; 52 of 89 surveyed pools (58.4%) were occupied. The same pattern holds for year 2007, which had the lowest precipitation in the first six months of the water year (1 October 2006–31 March 2007) in study meadows (Table 3) and also had the lowest percentage of occupancy by *A. canorus*; 44 of 124 surveyed pools (35.5%) were occupied. Even with the low precipitation and occupancy, the pattern of occupancy in year 2007 with regard to microhabitat variables was consistent. The occupied pools in this dry year had a higher water temperature, greater water depth, and greater amount of surface water than unoccupied pools (Fig. 2). These results from years 2005 and 2007 indicate that although larger-scale environmental conditions may vary, the microhabitat requirements for occupancy by *A. canorus* appear to be relatively constant despite varying precipitation.

**Effects of climate change.**—Pool microhabitat variables are related to surface and underground meadow hydrology. Hydrologic conditions are dynamic throughout the year and lead to pronounced changes in the meadow including in the pools. The majority of precipitation in the Sierra Nevada mountain range falls as snow between December and April, and as the snow melts, large areas of a meadow are flooded with surface water that fills small depressions to form pools. As the water year progresses, water recedes from these broadly inundated areas and depressions; desiccation may occur completely. The pattern and timing of dry down in the meadow and pools are affected by annual climate conditions, such as the amount of snow pack and timing of snowmelt, and local meadow conditions such as slope and aspect. Changes to the climate conditions will affect the hydrology and likely will impact the suitability of pools for toad occupancy.

Climate change projections show that the Sierra Nevada will have increased annual temperatures and reduced winter-spring snowpack in the coming decades (Cayan et al., 2008; Kapnick and Hall, 2010). The Sierra Nevada already has experienced a record low snowpack in 2015 (Belmecheri et al., 2015). These current and projected conditions likely will negatively affect the hydroperiod and suitability of pool microhabitats for eggs and tadpoles of *A. canorus*, and fewer pools will be occupied such as in the dry year in 2007. Lower pool occupancy is related to lower recruitment for the species. A concurrent study in most of the same meadows as our study shows that tadpole counts of *A. canorus* as well as newly metamorphosed young-of-the-year counts were lowest in year 2007 (McIlroy et al., 2013).

*Anaxyrus canorus* tends to be philopatric, with individual adults returning to the same meadow to breed each year (Brown et al., 2012). Within meadows, there is some site fidelity at the microhabitat-scale and individuals have been found to use the same pools in multiple years (Brown et al., 2012; Liang, 2013). If a pool is not suitable for breeding due to larger-scale environmental conditions, it is possible that individuals who historically have used that pool will not breed in that year. Even if the individuals use other breeding sites within the meadow, there might be increased competition for the available suitable pools both during breeding and larval development. These possibilities could lead to reduced population growth rate over time.

**Conclusion.**—Understanding habitat suitability for declining species can provide insight into causes of population declines if caused by habitat alteration. Identifying and protecting these habitats is a management goal for many species, although oftentimes the habitat is defined at a broad scale. The finer-scale microhabitat requirements often are not known or studied. Knowledge about microhabitats is critical for understanding species persistence, however, and provides information for effective protection of occupied habitat as well as for selection of suitable sites for re-introductions of rare species. By identifying and selecting re-introduction sites based on microhabitat characteristics that facilitate successful

<table>
<thead>
<tr>
<th>Water year</th>
<th>Six-month cumulative precipitation (inches) (1 October–31 March)</th>
<th>% of Average six-month cumulative precipitation (1961–2010)</th>
<th>% Occupied pools in study</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>44.7</td>
<td>132.8</td>
<td>58.4</td>
</tr>
<tr>
<td>2006</td>
<td>43.1</td>
<td>128.3</td>
<td>46.7</td>
</tr>
<tr>
<td>2007</td>
<td>20.6</td>
<td>61.4</td>
<td>35.5</td>
</tr>
<tr>
<td>2008</td>
<td>25.7</td>
<td>76.3</td>
<td>40.9</td>
</tr>
<tr>
<td>2009</td>
<td>31.8</td>
<td>94.7</td>
<td>47.2</td>
</tr>
<tr>
<td>2010</td>
<td>34.2</td>
<td>101.8</td>
<td>49.6</td>
</tr>
<tr>
<td>1961–2010</td>
<td>33.6</td>
<td>100.0</td>
<td>—</td>
</tr>
</tbody>
</table>
breeding and reproduction, wildlife managers can better ensure the success of the re-introduction.

Patterns of occupancy for *A. canorus* at the pool level reveal specific microhabitat requirements for breeding; wetted areas must have appropriate water temperature, water depth, and amount of surface water in order to be suitable for egg deposition and larval development. Detritus and vegetation also are important for toad microhabitats, although the mechanisms related to these relationships are not well understood. Overall, the differences in the physical microhabitat requirements between occupied and unoccupied sites are small but significant, and should be considered when looking at management options for this species at both the fine-scale and landscape-scale. At the fine-scale, the identification of suitable microhabitats within currently occupied meadows may help determine if protection or restoration of individual pools is necessary or feasible. At the landscape-scale, microhabitat characteristics can be one factor used in the overall evaluation of current and potential occupied meadows, such as when making decisions on where to allocate limited resources for restoration. The information from this study also indicates that the appropriate hydrolology within meadows is necessary for the formation of suitable microhabitats for toad persistence, and that the maintenance or restoration of historical hydrological processes within meadows could affect *A. canorus*.

ACKNOWLEDGMENTS

We thank the field crews for their work and contributions each year. Managers and biologists from the Sierra National Forest, Stanislaus National Forest, Forest Service Pacific Southwest Regional Office, and Yosemite National Park provided logistical support and invaluable help throughout the project; C. Brown provided helpful comments on the manuscript. We followed the guidelines set by the American Society of Ichthyologists and Herpetologists (Herpetological Care and Use Committee 2004) for handling of live amphibians. California Department of Fish and Game Scientific Collecting Permits were issued to RLG, KEV, and AJL. Funding was provided by the USDA Forest Service Pacific Northwest Research Station, U.S. Fish and Wildlife Service, Division, Rancho Cordova, California. AJL. Funding was provided by the USDA Forest Service Pacific Southwest Research Station, U.S. Fish and Wildlife Service, Division, Rancho Cordova, California.

LITERATURE CITED


