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WETLAND OCCUPANCY OF POND-BREEDING AMPHIBIANS IN YOSEMITE NATIONAL PARK, USA

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ABSTRACT: We estimated wetland occupancy and population trends for three species of pond-breeding anurans in Yosemite National Park from 2007 – 2011. We used a double survey technique in which two observers independently surveyed each site on the same day. Double surveys allowed us to calculate detectability for the three most common anurans within the park: *Rana sierrae*, *Anaxyrus canorus*, and *Pseudacris regilla*. Annual estimates of detectability were generally high; mean detectability ranged from 73.7% \pm 0.6 (SE) for any life history stage of *A. canorus* to 86.7% \pm 0.7 for sites with *P. regilla* reproduction (eggs or larvae present). Detectability was most variable for *Anaxyrus canorus*, which ranged from 45.9% to 99.7%. The probability of occupancy for *R. sierrae* was highest in larger, low-elevation wetlands that lacked fish. *Anaxyrus canorus* were more common in shallow high-elevation ponds; their occurrence was minimally impacted by the presence of fish. Finally, occurrence of *P. regilla* was largely unrelated to wetland size and elevation, but like *R. sierrae*, they were less likely to occupy sites with fish. Occupancy showed no trend over the five years of our study for *R. sierrae* or *A. canorus* when considering either sites with any life stage or only sites with reproduction. However, *P. regilla* showed a modest downward trend for sites with any life stage and sites with reproduction. Our results for *R. sierrae* run counter to expectations given recent concern about the decline of this species, while our findings for *P. regilla* raise concerns for this widespread and generally common species.

INTRODUCTION

Monitoring amphibians across large landscapes is challenging due to the logistical difficulties of sampling remote, rugged, and roadless areas. There are also technical difficulties in detecting target species that are only seasonally active and difficult to find in their natural environment. Yet distribution and population trends are the types of information most needed by land managers to assure that management practices are appropriate and effective. All these challenges are accentuated when working with rare species, which are often the species of greatest interest.

Amphibians are of particular concern because of the dramatic declines and extinctions that have been reported from many areas around the world (Stuart et al. 2004; McCallum 2007; Wake and Vredenburg 2008; Adams et al. 2013). One third of the world's amphibians are threatened with extinction, and 43% have declining populations (Stuart et al. 2004). The 2010 IUCN (International Union for Conservation of Nature) lists 486 species of amphibians as Critically Endangered, and as many as 159 amphibian species are likely to have gone extinct in recent years (IUCN 2010). Adams et al. (2013) monitored 48 species of amphibians for nine years at 34

study sites on Department of the Interior lands in the United States; they found that their study species were declining at a rate of 3.7% annually. They found that threatened species (i.e., IUCN red-listed species) were declining at 11.6% per year, and the rate of decline was highest on National Park Service lands, areas that are generally believed to be the best protected landscapes in the country.

Amphibian survey protocols that do not account for sites where amphibians were present but not detected result in occupancy estimates that are too low. This is of concern everywhere, but especially in the Sierra Nevada and Cascade Mountains of California where some of the most extensive amphibian declines have occurred (Fellers and Drost 1993; Drost and Fellers 1996; Knapp and Mathews 2000; Knapp 2005; Vredenburg et al. 2007). Knapp et al. (2003) addressed this by noting that during the summer, adults and larvae occur almost exclusively in shallow water near shore and are easily detected even in the deepest lakes. However, Beebee and Griffiths (2005) express concern about extrapolating from single counts such as these because the probability of detection can vary between observers, between habitats, and with different time periods. The pitfalls of ignoring detect-

ability have been addressed and methods for evaluating detectability are now readily available (MacKenzie et al. 2002; MacKenzie et al. 2003, MacKenzie et al. 2006). These techniques generally involve surveying each site twice (=double survey) during each site visit.

We used double surveys to evaluate the status of amphibians in Yosemite National Park, a large montane park in California. Based on resurveys of historic sites visited 75 years earlier by naturalists from the Museum of Vertebrate Zoology and the California Academy of Sciences, Drost and Fellers (1996) documented anuran declines in the Yosemite area. In response to this finding, and as part of the U.S. Geological Survey Amphibian Research and Monitoring Initiative (ARMI), we developed an amphibian monitoring program to assess amphibian status and trends within Yosemite N.P.

We report here on five years of annual surveys of 172 wetland sites in 14 randomly selected watershed units across Yosemite N.P. Double surveys were conducted at each site in each year, allowing us to estimate detection probabilities for each species and to examine factors related to detection. Controlling for detection, we report occupancy trends and predictors of occurrence for the three most common anurans within the park. We evaluated patterns of occurrence for sites with any life stage (i.e., adults, subadults, larvae, or eggs present) and for sites with reproduction (i.e., eggs or larvae present). We also evaluated the influence of elevation, fish, watershed, and wetland structure on occurrence probabilities.

MATERIALS AND METHODS

Study Area – We conducted our study at Yosemite N.P.,

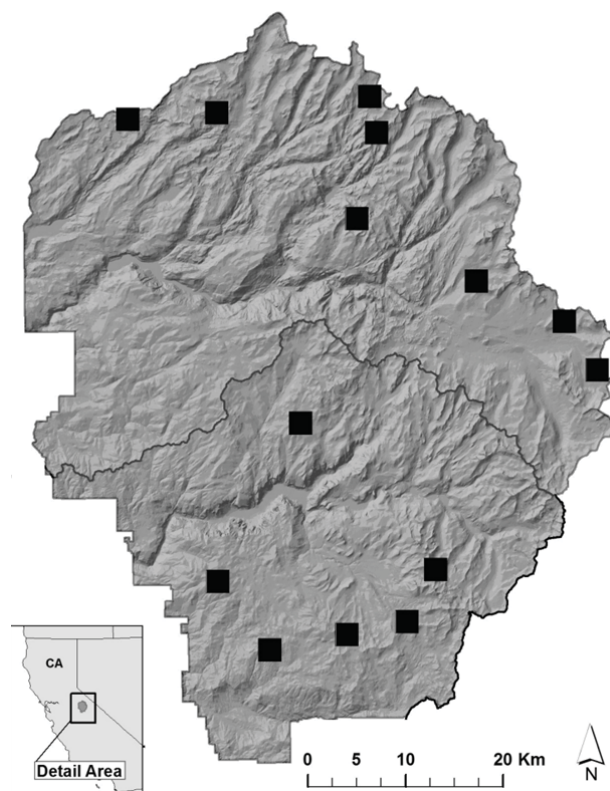


Figure 1. Location of 14 watershed units sampled for pond-breeding anurans in Yosemite National Park, 2007 – 2011. The Tuolumne watershed is north of the black line that runs through the center of the park, and the Merced watershed is to the south.

a 3,028 km² park with an elevational range of 648 – 3,997 m, located in the central Sierra Nevada mountains of California. There are two major river drainages within the park. The Tuolumne River in the north drains 1,731 km², while the Merced River drains 1,300 km² in the south, including Yosemite Valley. The predominant vegetation is lodgepole pine (*Pinus contorta*), and both red and white firs (*Abies concolor* and *A. magnifica*). At lower elevations there are other species of pines and riparian vegetation including willow (*Salix jepsonii*), corn lily (*Veratrum californicum*), small camas (*Camassia quamash*), and broad-leaf lupine (*Lupinus latifolius*). Yosemite receives the majority of its precipitation during the winter and early spring as snowfall (Serreze et al. 1999). Yosemite has been a National Park since 1890; visitation is high with over 4 million visitors per year. However, 94% of the park is designated as wilderness, with access via 1,300 km of trails. Most visitors only frequent areas immediately adjacent to roads, and overnight backcountry use within the park is regulated by a permit system.

Pond-breeding Anurans – Amphibian diversity in Yosemite is modest with only six pond-breeding anurans recorded within the park. Pacific treefrogs (*Pseudacris regilla*) are widespread, breeding in both permanent and ephemeral bodies of water throughout the park where they range up to 3,320 m elevation. Sierra Nevada yellow-legged frogs (*Rana sierrae*; formerly part of *R. muscosa*) are fairly widespread within Yosemite where they breed in permanent bodies of water at elevations ranging from 1,793 – 3,527 m. Yosemite toads [*Anaxyrus* (= *Bufo*) *canorus*] breed in both permanent and ephemeral water bodies, but generally avoid the larger lakes. *Anaxyrus canorus* are found in the park from 2,135 – 3,339 m elevation. All three of these species breed in the late spring or early summer as the snow melts, and are active until early fall. Each species employs a different reproductive strategy: *A. canorus* are explosive breeders with rapidly maturing larvae, *P. regilla* have a longer breeding season (approximately 6 weeks) with larvae that metamorphose into subadults by the end of the summer, and *R. sierrae* breed as the snow melts, but their larvae take at least three years to metamorphose into subadults at these elevations.

Three other anuran species were not sufficiently common or widespread to include in our study. California red-legged frogs (*Rana draytonii*) have been extirpated from the few sites where they once occurred, though historic populations within the park may have been introduced (Barry and Fellers 2013). Western toads (*Anaxyrus boreas*) occur in Yosemite Valley (1,200 m), but we have located only one individual during the 38 surveys conducted in Yosemite Valley over the last 19 years (pers. obs.). The non-native American bullfrog (*Lithobates catesbeianus*) occurs in Yosemite Valley as well as at a few low elevation (< 1,500 m) sites west of Hetch Hetchy Reservoir (pers. obs.).

Watershed Units – Using 7.5' U.S. Geological Survey topographic maps, we divided the park into 220 watershed units. Each watershed unit encompassed 10 – 25 potential anuran breeding sites, e.g. ponds, lakes, meadows with pools. The number of sites per watershed varied depending on the size of the sites, but total survey effort was similar between all watershed units. The boundaries between watershed units followed natural features and drainages whenever possible. A few large valleys had to be subdivided because of the large number of potential breeding sites. In those areas, we used natural groupings of nearby water bodies as a guide to drawing boundaries.

We divided the sampling units between the two river basins based on area, and randomly selected six watershed units from the Merced River basin, and eight from the larger Tuolumne River basin (Table 1, Figure 1) that were within the historic range of *R. sierrae*, *A. canorus*, and *P. regilla*. From 2007 – 2011, we surveyed all 172 wetland sites within the 14 watershed units each year.

Survey Methods – We used Visual Encounter Surveys (Crump and Scott 1994) to search for amphibians at each potential breeding site. Equipped with a dip net and binoculars, a biologist slowly walked around the perimeter of the site looking for eggs, larvae, subadult, and adult anurans. Separate tallies were maintained for each life history stage of each of the three pond-breeding species.

Each site was surveyed by two biologists, providing two independent assessments of species presence. Surveys were conducted using the following protocol designed to maximize the independence of our double samples,

while minimizing environmental variation between surveys. There was a 15 – 60 min delay between the first and second survey to allow time for anurans to recover from disturbance caused by the initial pass. Delays longer than 60 min might result in weather changes that could affect amphibian activity and detection. The biologists were not allowed to observe each other so that no clues were obtained about whether amphibians were being detected. The biologists did not discuss the results of the surveys until both surveys had been completed. Finally, the biologists alternated who did the first survey.

At the time of each survey, we recorded observer name, first or second survey, water temperature, maximum water depth (truncated at 3 m), and site dimensions. Additional covariates were subsequently recorded for each site: river basin (Tuolumne versus Merced), elevation, presence of fish (non-native trout), and days after snowmelt was complete. Yosemite N.P. provided records of fish presence based on gill net surveys conducted by Ro-

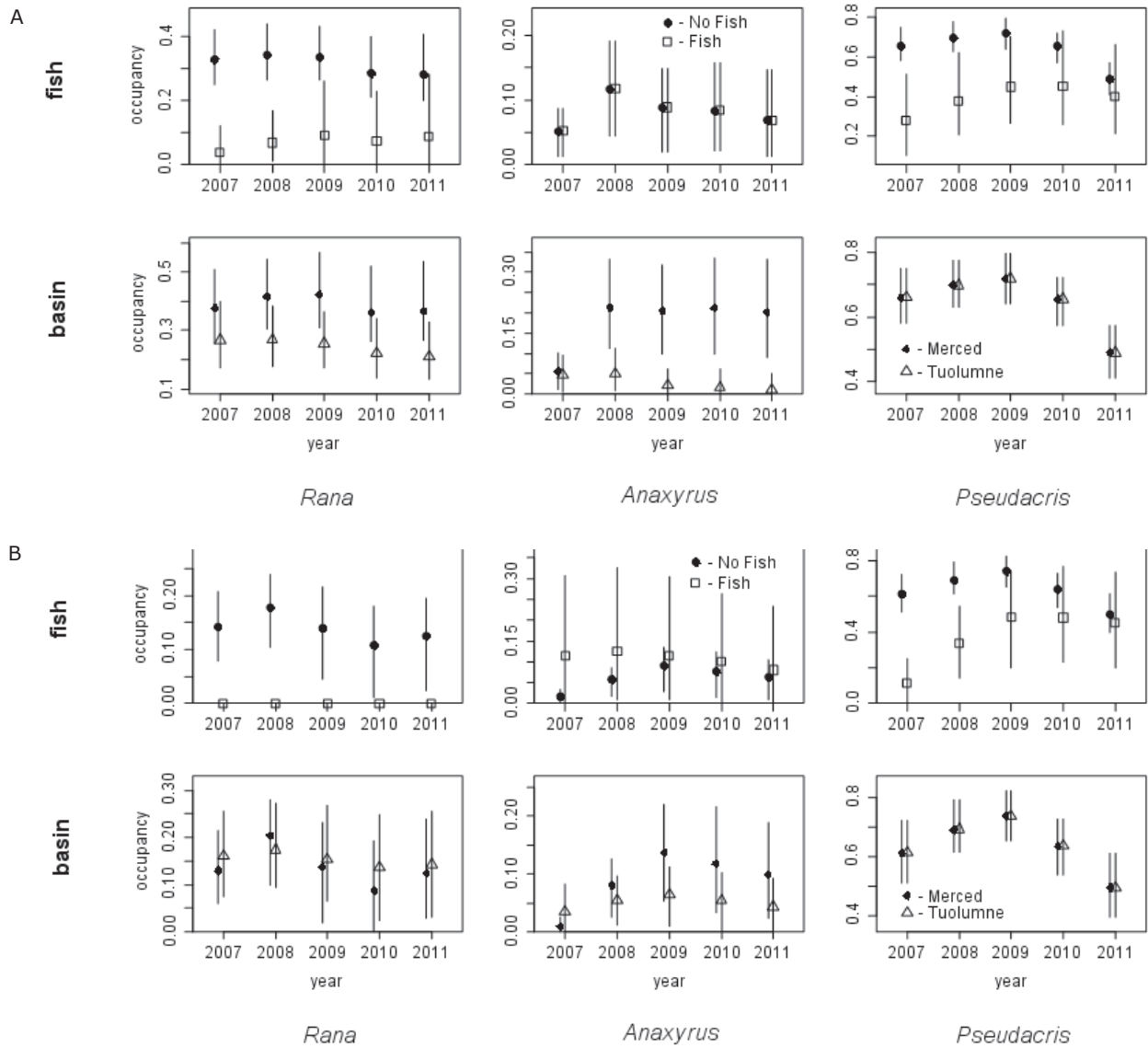


Figure 2. Comparison of occupancy and 95% confidence intervals for sites with (unfilled squares) and without (filled circles) introduced trout for *Rana sierrae*, *Anaxyrus canorus*, and *Pseudacris regilla* for each year of the study, and occupancy by basin: Tuolumne (unfilled triangles) and Merced (filled circles). A. Any life history stage, B. Sites with reproductive stages.

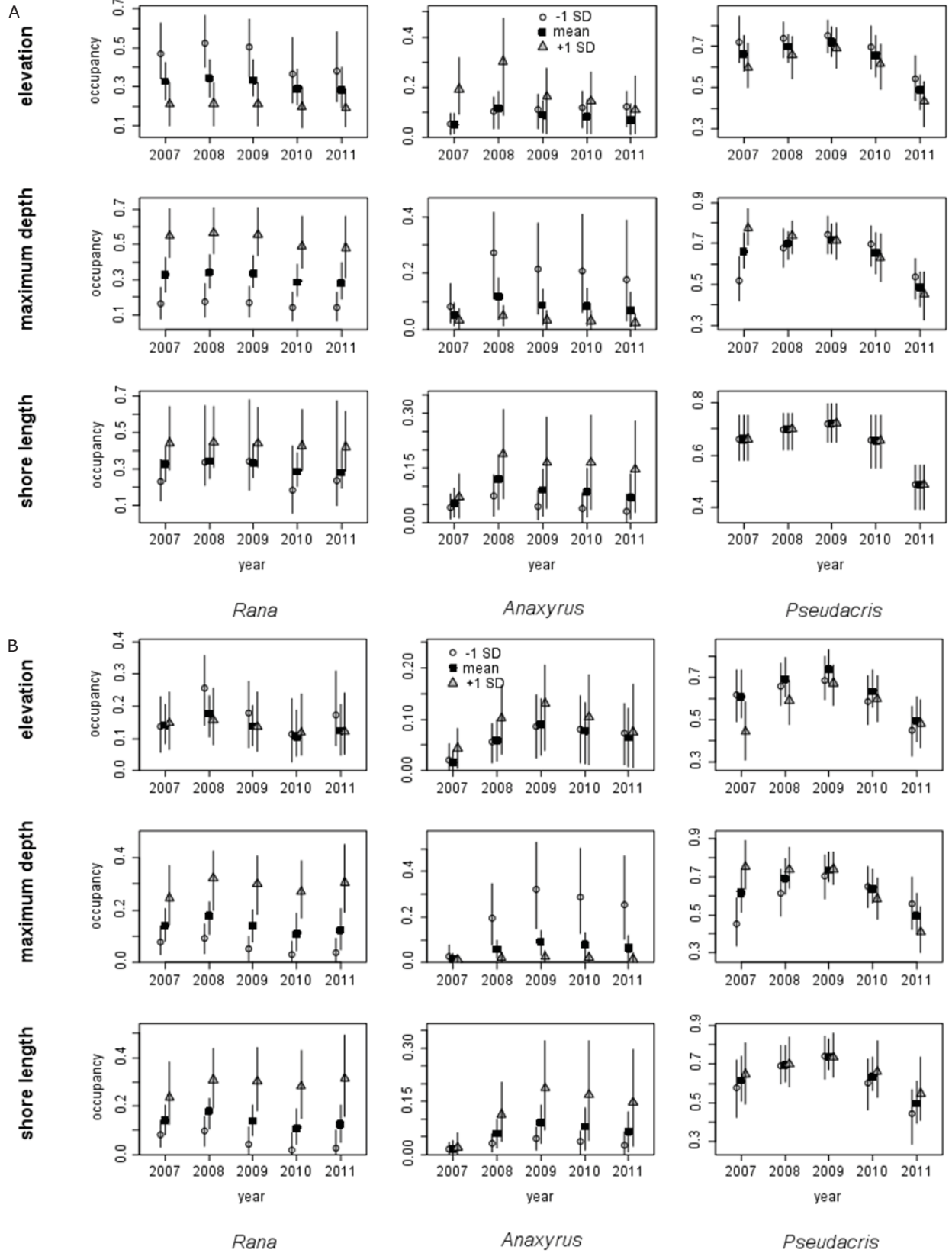


Figure 3. Comparison of occupancy probabilities and 95% confidence intervals of *Rana sierrae*, *Anaxyrus canorus*, and *Pseudacris regilla* in sites where fish were not present. For each covariate (elevation, maximum depth, or shore length) we plot occupancy probabilities for sites at the mean covariate value (black square) and for sites where the covariate value was one standard deviation above (gray triangle) or below (unfilled circle) the mean covariate value. A. Any life-history stage, B. Sites with reproductive stages.

Table 1. Watershed units (n = 14) and number of sites (e.g., ponds, lakes, meadows) sampled for pond-breeding anurans in Yosemite National Park, 2007–2011.

Watershed Unit	Survey Sites	River Drainage	Mean Elevation (m)
Buena Vista	13	Merced	2667
Gray Peak	16	Merced	3042
Merced Pass	14	Merced	2751
Porcupine Flat	13	Merced	2509
Summit Meadow	9	Merced	2199
Turner Meadows	9	Merced	2390
Bartlett Peak	11	Tuolumne	2460
Dana Meadows	16	Tuolumne	2999
Kerrick Meadow	9	Tuolumne	2851
Otter Lakes	20	Tuolumne	2737
Parker Pass	10	Tuolumne	3245
Young Lakes	11	Tuolumne	2978
Rock Island Lake	10	Tuolumne	2988
Rodgers Lake	11	Tuolumne	2871
Total	172		

land Knapp. We used a snow sensor at Gin Flat (2,070 m elevation) in the Merced River basin as a standard for determining when the snow had melted each year. Days after snowmelt was then calculated as the number of days between when there was no snow at Gin Flat and the date of each survey. Days after snowmelt is a more meaningful metric than calendar date because amphibian activity in Yosemite N.P. is closely tied to time of snowmelt (pers. obs.), which can vary from year to year due to large differences in winter snowfall.

All field work took place within Yosemite N.P. and was authorized by annual research permits issued by the park. Animals were captured only when necessary to confirm identification; each individual was then released after < 1 min at the point of capture.

Statistical Methods – We estimated probabilities of occurrence for each species using dynamic occupancy models (MacKenzie et al. 2003). The approach accounts for incomplete detection, and allows us to estimate occupancy of wetlands as a function of whether the site was occupied in the previous year. Estimated parameters include the probability that a species will be detected at a site given that the site is occupied (p), the initial probability a site is occupied (ψ_0), the probability an occupied site was unoccupied in the following year (ϵ_t), and the probability an unoccupied site was occupied in the following year (γ_t). We evaluated the relationship of each of these parameters to covariates using generalized linear models with a logit-link function (MacKenzie et al. 2002).

For each of the three species, we modeled the probability that the species occurred at a site based on observations of any life stage, and the probability that reproduction occurred at the site based on observations of eggs or larvae. For each of the six combinations, we fit models based on a set of factors we hypothesized would affect detection and another set of factors we hypothesized would affect occupancy (initial occupancy, extinction, and colonization; Appendix, Table S1). We used these factors to develop candidate models for both detection (4 models) and occupancy (32 models). In the case of initial occupancy and transition parameters, we only included models in which covariates affected all three parameters simultaneously (ψ_0 , ϵ_t , and γ_t). We selected among alternative models based on Akaike's Information Criterion (AIC). In selecting among alternative models, we used a two-step approach. We began by considering alternatives for the detection parameter while using the full

parameterization for occupancy parameters (all effects model). We then fixed the detection parameters, using the parameterization with the lowest AIC value from the first step, and compared fit for alternative parameterizations of occupancy.

We hypothesized that detection would differ by year, the number of days after snowmelt, observer, and water temperature. For initial occupancy and transition parameters we considered the effect of river basin (Tuolumne versus Merced River), linear and quadratic functions of elevation, maximum water depth, and shore length, as well as whether fish were present. Including both linear and quadratic functions for elevation allowed us to test whether there was a consistent trend in occurrence across all the elevations observed (linear) or whether there was an optimal elevation where occurrence was highest (quadratic). In addition, we included an effect for annual differences in all extinction and colonization models.

We fit models using the `colect` function in the unmarked package (Fiske et al. 2011) in R (v. 2.14.1; R Core Development Team 2011). Occupancy probabilities after the initial year were calculated as a function of estimated transition probabilities (ϵ_t and γ_t). We used a parametric bootstrap procedure to estimate standard errors and confidence intervals for occupancy probabilities. In addition, we calculated the relative change in occupancy from the first to final year of the study ($\lambda = \Psi_{2011} / \Psi_{2007}$).

To facilitate comparisons among effect sizes, all continuous covariates were standardized prior to analyses to have a standard deviation (SD) of 1. Thus, estimated effect sizes were the rate of change in the parameter with respect to a 1 SD change in the covariate. In addition, to quantify the expected effect on occupancy of covariates affecting transition rates, we calculated the sensitivity of equilibrium occupancy to changes in each of the continuous covariates (Miller 2012). Sensitivities for each individual covariate were calculated at the mean value for all additional covariates. These sensitivities can be interpreted as the expected magnitude of change in long-term occupancy, given a small change in the covariate value. This allows for a more direct interpretation of effect sizes compared with examining the relationship of a covariate to transition probabilities (Miller 2012).

RESULTS

The three most common species of pond-breeding anurans in Yosemite N.P. were used in our analysis: *R. sierrae*, *A. canorus*, and *P. regilla*. We evaluated detectability of these species using double survey data, where a value of 100% would indicate that if one survey detected a species, the companion survey also did so on every occasion. Mean annual detectability across all five years ranged from 73.7% \pm 0.6 (SE) for any life history stage of *A. canorus* to 86.7% \pm 0.7 for sites with *P. regilla* reproduction (eggs or larvae present; Table 2). Year-to-year variation in detectability was low for *P. regilla*, whether considering any life stage or only those sites with reproduction. *Rana sierrae* detectability was both intermediate and consistent. *Anaxyrus canorus* had the most variable detectability, both for any life stage and at sites with reproductive stages. *Anaxyrus canorus* also had both the lowest (45.9%) and the highest (99.7%) detectability for any of the three species (Table 2).

For the six combinations of species and life history stage, detectability was influenced by one or several of the covariates we hypothesized might be important:

Table 2. Site occupancy of pond-breeding anurans in 14 Yosemite National Park watershed units from 2007 – 2011. Values are the percentage of sites where the species was detected during the initial survey (single survey), estimated percentage of occupied sites where the species was detected (detectability) during a single visit, and estimated percentage of sites that were occupied (occupancy) when we accounted for imperfect (<100%) detection. We estimated probabilities for any life history stage and for a subset of sites that included reproduction (eggs and/or larvae).

Species / Year	Any life stage			Reproductive stages		
	Single Survey	Detectability (p)	Occupancy (ψ)	Single Survey	Detectability (p)	Occupancy (ψ)
<i>Rana sierrae</i>						
2007	27.9	87.1	32.0	12.2	88.4	14.3
2008	23.2	73.3	36.1	13.4	69.1	19.9
2009	25.0	75.3	34.8	13.4	82.3	15.9
2010	21.5	73.7	27.1	12.2	89.5	13.4
2011	25.0	76.6	29.6	13.4	81.7	15.9
Mean (SE)	25.7 (1.7)	77.2 (2.5)	31.9 (1.6)	13.5 (0.3)	82.2 (3.6)	15.9 (1.1)
<i>Anaxyrus canorus</i>						
2007	12.2	88.8	18.3	7.6	99.7	7.9
2008	17.4	64.3	27.3	12.8	65.4	16.6
2009	21.5	84.0	23.0	16.9	80.8	20.5
2010	14.0	56.0	23.8	9.3	45.9	18.2
2011	16.3	75.3	21.9	14.0	91.1	15.0
Mean (SE)	16.9 (1.4)	73.7 (6.1)	22.9 (1.5)	12.5 (1.5)	76.6 (9.6)	15.6 (2.1)
<i>Pseudacris regilla</i>						
2007	51.7	82.9	72.4	43.0	86.1	55.6
2008	56.9	84.3	69.1	50.0	84.9	60.0
2009	59.3	85.5	70.5	55.8	85.7	65.3
2010	55.2	86.6	61.4	46.5	88.0	56.4
2011	45.3	88.0	48.0	41.3	88.6	44.5
Mean (SE)	56.0 (2.7)	85.5 (0.9)	64.3 (4.5)	51.3 (3.2)	86.7 (0.7)	56.4 (3.4)

year, water temperature, days after snowmelt, and observer (Table 3). Water temperature was included in the best detection model for all but *R. sierrae* reproduction and in all species and life stages detectability was positively correlated with increased water temperature. Year occurred in all the best models for *R. sierrae* and *A. canorus*, but not *P. regilla*. Instead observer and days after snowmelt were in the best detection models for *P. regilla*. Estimates of parameters in the best model for each species are summarized in Table 4. Days after snowmelt was included in the highest ranking models for *P. regilla*, but not for *A. canorus*, which has a very short breeding season just as the snow melts at breeding sites, or for *R. sierrae*, which has larvae that overwinter and do not metamorphose until the third summer.

Occupancy was influenced by all five covariates we examined (Table 5 and 6). For all six species and life stage combinations, maximum depth and either elevation or elevation² were included in the best model. Shore length and the presence of fish (non-native trout) were included in five of the best models. River basin (Tuolumne versus Merced) was in the best model for the any life stage analysis and for reproductive stages for *A. canorus* and *R. sierrae*, but not for *P. regilla*, while elevation took a quadratic form in both analyses of *A. canorus* and for sites with *P. regilla* reproduction. Similarly, the presence of fish was an important predictor for all but the any life stage analysis for *A. canorus*. Estimates of parameters in the best model for each species are summarized in Table 6. Elevation had the largest effect on all three species, though the effect was negative (lower occupancy at higher elevations) for *R. sierrae* and *P. regilla*, and positive for *A. canorus*. Maximum depth showed the same pattern, positive for *R. sierrae* and *P. regilla*, and negative for *A. canorus*.

Mean occupancy across all years and sites for any life stage was 22.9% for *A. canorus*, 31.9% for *R. sierrae*, and 64.3% for *P. regilla*. Restricting occupancy to those

sites with reproduction resulted in mean occupancy rates of 15.6% for *A. canorus*, 15.9% for *R. sierrae*, and 56.4% for *P. regilla* (Table 2). We saw an increase in occupancy from the first to last year for any life stage of *A. canorus* ($\lambda = 1.53$ CI = 1.02 – 2.10) and a decrease for *P. regilla* ($\lambda = 0.80$ CI = 0.66 – 0.98), while *R. sierrae* was relatively similar for the first and last years ($\lambda = 0.93$ CI = 0.71 – 1.17). Reproductive occupancy similarly increased for *A. canorus* ($\lambda = 1.94$ CI = 1.26 – 3.21), while confidence intervals for *P. regilla* ($\lambda = 0.94$ CI = 0.75 – 1.15) and *R. sierrae* ($\lambda = 1.16$ CI = 0.84 – 1.57) both included 1, the expected value if there was no trend in occupancy across years.

The presence of introduced fish had a negative impact on occupancy for both *R. sierrae* and *P. regilla* when examined either for any life stage or only for sites with reproduction. In the case of *R. sierrae*, although we observed adults at some sites where fish were present, we never observed reproduction at sites with fish. Fish did not appear in the best model for any life stage of *A. canorus*, but the presence of fish was positively related to occupancy of *A. canorus* reproductive stages (Figure 2, Tables 5 and 6). Occupancy was higher in the Merced basin for any life stage of *R. sierrae* and for any life stage and reproductive stages (except in 2007) of *A. canorus* (Figure 2).

We examined the relationship between shore length, maximum depth, and elevation on occupancy for all three anurans (Figure 3). All three variables had negligible effects on *P. regilla* occupancy. *Rana sierrae* tended to occupy lower elevations, but there was little difference in elevation for sites where *R. sierrae* reproduced. Occupancy probabilities for *A. canorus* were initially lower at low elevations. However, the relationship between occupancy and elevation became negligible in later years. Occupancy rates were greater for *R. sierrae* (both any life stage and reproduction) at sites with longer shore lengths, while *A. canorus* were more likely to occupy

Table 3. Detection models for each combination of species and life stage. Temperature = water temperature, date = days after snowmelt at our Gin Flat reference site. AIC = Akaike's Information Criterion. All models with $\Delta AIC < 4$ are presented; k = number of parameters.

	Model	ΔAIC	AIC	k
Any Life Stage				
<i>Rana sierrae</i>	year, temperature	0.00	1063.55	33
	year	2.83	1066.38	32
	observer, date, temperature	3.45	1067.00	40
<i>Anaxyrus canorus</i>	year, temperature	0.00	849.61	33
<i>Pseudacris regilla</i>	observer, date, temperature	0.00	1595.09	40
	year, temperature	0.75	1595.84	33
Reproductive Stages				
<i>Rana sierrae</i>	year	0.00	562.21	32
	year, temperature	1.29	563.49	33
<i>Anaxyrus canorus</i>	year, temperature	0.00	589.21	33
<i>Pseudacris regilla</i>	observer, date, temperature	0.00	1429.61	40

sites with shallower wetlands, but tended to occupy wetlands with longer shore lengths.

DISCUSSION

Prior amphibian surveys – Extensive surveys for pond-breeding amphibians have been conducted in the Sierra Nevada and Cascade Mountains of California. It has been widely assumed either implicitly (Fellers and Drost 1993; Drost and Fellers 1996) or explicitly (Knapp and Mathews 2000; Knapp 2005; Vredenburg et al. 2007) that single surveys were a good indication of presence, but there have been almost no attempts to confirm this assumption. Brown and Olsen (2013) assumed population closure over an 8-year period (2002 - 2009) and used surveys repeated over multiple years to estimate detectability of *A. canorus* and *Rana* in the *R. sierrae/muscosa* species complex. While detectability was > 80% for *A. canorus* surveys conducted early in years with at least normal snowfall, detectability dropped to near zero for mid- to late-summer surveys in low snowfall years. Detectability was not as sensitive to time of year for *R. sierrae/R. muscosa* species pair, but detectability dropped from a high of 80% for mid- or late-summer surveys in years with little snow to < 20% in years with heavy snow (Brown and Olsen 2013). In our study, we used surveys repeated by a second observer on the same day and found that detectability was high for all three of the anurans in Yosemite N.P., ranging from a mean of 73.7% (any life stage of *A. canorus*) to 86.7% (reproductive stages of *P. regilla*). *Rana sierrae*, which is a close relative of *R. muscosa*, ranged from a mean of 77.2% for any life stage to 82.2% for sites with reproduction. These results are important because they add credibility to the largely untested assumption that anurans occupying high elevation sites in the Sierra Nevada are readily detectable, and hence surveys that extend back to at least 1992 (Drost and Fellers 1996) should be a good indication of amphibian occurrence. However, detectability should be accounted for in study designs for Sierran amphibian studies whenever possible.

Detectability implications – Although detectability was generally high in our study, we did observe differences as a function of year, water temperature, and observer. While adults of these montane anurans can be active at low temperatures, especially during the breeding season [e.g., adult *R. muscosa* traversing over snow (Pope and Matthews 2001), and adult *P. regilla* calling at 0° C (pers. obs.)], the larvae are more active and more detectable at higher water temperatures. Our results reinforce our survey protocol, which specifies that surveys not be conducted when environmental temperatures are low.

Not all observers are equally skilled at detecting vertebrate species, whether they be birds (Sauer et al. 1994; Farmer et al. 2012), snakes (Dorcas and Willson 2009), or frogs (Gooch et al. 2006; Pierce and Gutzwiller 2007; Miller et al. 2012). In our study, observer was a high ranking covariate only for *P. regilla*, the most frequently encountered anuran. Although observer was not included in the best model for the other species, we may have had limited power to estimate differences among 12 observers for the less common *R. sierrae* and *A. canorus*.

Year was the second most common covariate that influenced detectability for all three species, whether considering any life stage or only reproductive stages. Year probably reflected a combination of factors including annual snow accumulation, variation in observer ability, and changes in average abundance. *Pseudacris regilla* larvae were often abundant at sites where they bred, which led to high detectability that was probably not related to year. However, detectability can sometimes decrease as population size decreases (Tanadini and Schmidt 2011). Also, while many of our field crew members worked in multiple years, there was some annual turnover. Differences in each observer's ability to find amphibians may have contributed to year being an important variable.

Site occupancy in Yosemite – Site occupancy was highest for *P. regilla* and lowest for *A. canorus*, with *R. sierrae* somewhat higher than *A. canorus*. This pattern held true when calculating site occupancy for any life stage, or for those sites with reproduction. These findings are similar to Knapp (2005), though our survey and analytical techniques were somewhat different. Most notably, Knapp used single site surveys that did not account for detectability; hence his occupancy estimates were negatively biased because they were not corrected for imperfect detection. Knapp (2005) reported that *R. sierrae* reproductive stages (eggs, larvae, or recent metamorphs) were found at 11%, *A. canorus* at 3%, and *P. regilla* at 57% of the 2,655 sites surveyed in Yosemite N.P. between 2000 and 2002. These numbers were similar to our uncorrected single surveys that detected eggs or larvae at a mean of 13.5, 12.5, and 51.3% from 2007 - 2011 for those same species. Because we restricted our surveys to watershed units that were within the historic range of *R. sierrae*, all of which were also within the geographic range of both *A. canorus* and *P. regilla*, one would expect our estimates of occupancy to be somewhat higher than those of Knapp (2005), who included all lentic water bodies in Yosemite N.P. Also, his inclusion of recent metamorphs (versus our inclusion of only eggs and larvae) probably increased the number of sites where he reported reproduction. While

Table 4. Estimated effects (SE) for detection covariates. Temperature = water temperature, date = days after snowmelt at our Gin Flat reference site. Annual effects are relative to 2007. Estimates are only given for effects in the best model. Observer effects are not included.

Parameter	Any Life Stage			Reproductive Stages		
	Rana	Anaxyrus	Pseudacris	Rana	Anaxyrus	Pseudacris
2008	-0.96 (0.42)	-1.64 (0.82)	****	-1.22 (0.57)	-34.55 (1.54)	***
2009	-0.77 (0.43)	-0.35 (0.71)	****	-0.49 (0.62)	-33.56 (1.52)	****
2010	-0.77 (0.46)	-1.72 (0.58)	****	0.11 (0.69)	-35.13 (1.48)	****
2011	-0.61 (0.46)	-0.77 (0.63)	****	-0.5 (0.62)	-32.48 (1.63)	****
temperature	0.29 (0.13)	0.51 (0.20)	0.60 (0.11)	****	0.49 (0.17)	0.54 (0.13)
date	****	****	0.41 (0.11)	****	****	0.53 (0.14)

**** = covariates that did not appear in the best model.

the magnitude of this is difficult to evaluate, it is likely fairly small. The effect would be the least for *R. sierrae* because they overwinter as larvae and metamorphose at the end of the third summer; hence, reproductive stages are present at breeding sites all year long (Vredenburg et al. 2005). By contrast, *A. canorus* spend the shortest amount of time at breeding sites (Karlstrom 1962; Kagarise Sherman 1980). Knapp (2005) reported *A. canorus* reproduction at only 3% of sites compared with our uncorrected 12.5%. When correcting for detectability, we had a five-year mean of 15.6% of sites occupied by *A. canorus* reproductive stages, and 22.9% of sites occupied by any life stage. *Anaxyrus canorus* detectability was quite variable in our study, ranging from 45.9 – 99.7% (Table 2), but it is unlikely that detectability was consistently low throughout the three years of Knapp's study. While we did not see an increase or decrease in occupancy (Ψ) during the five years of our study (2007 – 2011), it is possible that *A. canorus* occupancy increased during the five-year interval between our surveys and those of Knapp (2005).

Single survey occupancy estimates for *R. sierrae* varied little between Knapp's 2000 – 2002 surveys and our 2007 – 2011 surveys. Furthermore, we found no significant change in occupancy of either sites with reproduction or any life stage for *R. sierrae*. This would not be the expected pattern given recent concerns about the decline of *R. sierrae* and the closely related *R. muscosa* in the southern Sierra Nevada (Vredenburg et al. 2010). However, it is quite possible that significant *R. sierrae* declines occurred in Yosemite prior to recent amphibian studies by Drost and Fellers (1996), Knapp (2005), and our present study. This hypothesis would be supported by an eight-year study of a *R. sierrae* population in a large meadow system (Summit Meadow) in Yosemite N.P. (Fellers et al. 2013) where there were annual fluctuations in population size, but no overall decline. Ongoing monitoring of all the watershed units in our study, and ongoing mark-recapture of *R. sierrae* at Summit Meadow will hopefully shed light on population trends in Yosemite.

Brown and Olsen (2013) studied *A. canorus* and *R. sierrae/muscosa* in the Sierra Nevada, but it is difficult to make comparisons with their findings. Their work spanned 625 km of the Sierra Nevada (including areas surrounding Yosemite N.P.) and the Cascade Mountains. Also, their data were analyzed assuming closed populations over the eight years of the study. Though they accounted for detectability when estimating occupancy, detectability was calculated with surveys repeated in subsequent years, not on the same day. Their occupancy estimates for any life stage for drainage basins (not sites) ranged from 66 – 86% for basins within the range of *A. canorus*, and 29 – 47% of basins with *R. sierrae/muscosa*. Similar to our study, however, Brown and Ol-

sen (2013) did not find declines in *Rana* occupancy.

Pseudacris regilla was the only species where occupancy declined during our study. While there was no significant trend for sites with reproduction, there was a significant decline for sites with any life stage. That pattern was not caused by drought. In years with less than average snowfall, some *P. regilla* breeding sites dry up before larvae can metamorphose. During the five years of our study, there was more snow each winter, which would allow small ponds to persist longer, thus providing better *P. regilla* habitat each year. However, five years may not be a long enough period to observe subtle population trends for any of our study species. We will continue to track population trends throughout Yosemite N.P.

The pattern we observed for *P. regilla* cannot be compared with that of Knapp (2005) because he only reported on sites where *P. regilla* had reproduced. However, when comparing 1915 surveys by Grinnell and Storer (1924) and subsequent surveys at the same study sites in 1992, Drost and Fellers (1996) reported a decline in abundance for *P. regilla* at high elevation (> 1500m) sites. While a decrease in abundance is different from a decrease in sites occupied, it is the only other study to suggest that there might be concern for *P. regilla*, one of the more common species of amphibian in the Sierra Nevada and elsewhere in California.

Outside of Yosemite N.P., there have been only limited studies of amphibian occupancy in the Sierra Nevada. Knapp et al. (2003) reported that during 1995 – 1997, only 238 (14%) of 1,718 water bodies were occupied by *R. sierrae/muscosa* throughout their study area which included the John Muir Wilderness (Sierra National Forest) and Kings Canyon National Park, an area that extends from near the southeast corner of Yosemite N.P. to about 160 km south. This occupancy rate is only slightly higher than the 11% found by Knapp (2005) in Yosemite in 2000 – 2002. The difference is not likely to be significant, and might be explained by the inclusion of any life stage in the earlier study compared with only reproductive stages in Yosemite surveys. However, 14% is markedly lower than the 21.9 – 32.2% occupancy (mean = 25.7%) for the *R. sierrae* that we found for sites with any life stage during our initial (first of two) surveys at each site. Correcting for detectability, our estimates of occupancy ranged from 27.1 – 36.1% (mean = 31.9%) for any life stage. While there could be changes in occupancy in the decade between the Knapp et al. (2003) study and ours, it is also possible that occupancy is higher in Yosemite N.P. compared with areas farther south. This could be due to greater exposure to pesticides (Sparling et al. 2001) or differences in exposure to the amphibian chytrid fungus, *Batrachochytrium dendrobatidis*.

Factors affecting occupancy – Drainage basin (Tuolumne versus Merced) was an important covariate for both *R. sierrae* and *A. canorus*. This is seen most conspicuously for

Table 5. Occupancy models for each combination of species and life stage. All models with $\Delta AIC < 4$ are presented; k = number of parameters.

	Model	ΔAIC	AIC	k
Any Life Stage				
<i>Rana sierrae</i>	basin, elevation, max depth, shore length, fish	0.00	1060.04	30
	basin, elevation ² , max depth, shore length, fish	3.51	1063.55	33
<i>Anaxyrus canorus</i>	basin, elevation ² , max depth, shore length	0.00	847.92	30
	basin, elevation ² , max depth, shore length, fish	1.69	849.61	33
<i>Pseudacris regilla</i>	elevation, max depth, fish	0.00	1581.74	31
Reproductive Stages				
<i>Rana sierrae</i>	basin, elevation, max depth, shore length, fish	0.00	559.36	29
	elevation, max depth, shore length, fish	2.07	561.43	26
	basin, elevation ² , max depth, shore length, fish	2.85	562.21	32
<i>Anaxyrus canorus</i>	basin, elevation ² , max depth, shore length, fish	0.00	589.21	33
	elevation ² , max depth, shore length, fish	1.16	590.37	30
	basin, elevation ² , max depth, shore length	1.45	590.66	30
	elevation ² , max depth, shore length	1.62	590.82	27
	basin, elevation, max depth, shore length, fish	2.24	591.44	30
	basin, elevation, max depth, shore length	3.74	592.94	27
	elevation, max depth, shore length, fish	3.88	593.08	27
<i>Pseudacris regilla</i>	elevation ² , max depth, shore length, fish	0.00	1427.53	37
	elevation, max depth, shore length, fish	1.30	1428.82	34
	elevation ² , max depth, fish	1.41	1428.94	34
	basin, elevation ² , max depth, shore length, fish	2.09	1429.61	40
	basin, elevation, max depth, shore length, fish	2.09	1429.62	37
	basin, elevation ² , max depth, fish	3.46	1430.99	37

A. canorus at sites with any life stage (Fig. 2A), where for the last four years of the study, *A. canorus* occupied significantly more sites in the Merced compared to the Tuolumne River basin. It is unclear why this might be the case, and why it was not so in 2007, the first year of our study. This is a potentially important trend that we will monitor as the study continues.

Four occupancy covariates related to physical characteristics of sites: maximum water depth, shore length, and both the linear and quadratic functions of elevation. For *R. sierrae*, elevation and maximum water depth had the greatest effect, and elevation was negatively related to occupancy with lower occupancy at higher elevations. Knapp (2005) found a similar positive relationship with maximum water depth, which would be expected given that *R. sierrae* larvae overwinter twice before metamorphosing at the end of their third summer. The positive relationship of occupancy and shore length indicates that *R. sierrae* are occupying larger sites, which would also be expected because larger sites are more likely to hold water for multiple years and be suitable for reproduction and overwintering (Pope and Matthews 2001). Previous studies of *R. sierrae* have found both a positive and negative relationship with elevation (Knapp et al. 2003; Knapp 2005). These differences were attributed to not having sampled the full elevational range of *R. sierrae* (Knapp 2005); however, our study and that of Knapp both took place in Yosemite N.P., yet we had differing results. While it is possible that *R. sierrae* populations in Yosemite at higher elevations suffered declines between our two studies, the influence of elevation remains unclear.

There are no native fish throughout the higher elevations of Yosemite N.P., including all the watershed units in our study. However, five species of non-native trout have been widely introduced in the Sierra Nevada, including Yosemite N.P., where brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) are by far the most common species (Knapp and Matthews 2000; Knapp 2005). Consistent with prior studies, we found that the presence of fish had the greatest negative effect

on *R. sierrae* and *P. regilla*, while the relatively toxic *A. canorus* (Grasso et al. 2010) was less affected (Bradford 1989; Knapp and Matthews 2000; Knapp 2005).

Amphibian population trends – Previous studies have documented dramatic amphibian declines in the Yosemite area since the early 1900s (Drost and Fellers, 1996). However, our study found that only one of our three study species, *P. regilla*, had a downward trend during 2007 – 2011, continuing a pattern first noted by Drost and Fellers (1996). Documenting population trends is important, but it is essential to identify causative factors so their impact on amphibians can be mitigated. In particular, we need to better understand the role of amphibian chytrid (*Batrachochytrium dendrobatidis*) and environmental contaminants. Dramatic declines and complete extirpation of *R. sierrae* and *R. muscosa* populations have been closely associated with the arrival of amphibian chytrid in local populations (Briggs et al. 2005). However, some populations of *R. sierrae*, *A. canorus*, and *P. regilla* in Yosemite have persisted and apparently thrived with chytrid being present in a high proportion of individuals (Fellers et al. 2011). Also, *Rana sierrae* at Summit Meadow in Yosemite N.P. have maintained a large population even though chytrid has been present since at least 1999 (Fellers et al. 2013). Hence, while chytrid is clearly having a negative impact on many anuran populations, its current impact on anurans in the Yosemite area is less clear.

Environmental contaminants such as pesticides, herbicides, and fungicides are another possible factor in the initial decline of amphibians in the Sierra Nevada (Sparling et al. 2001; Angermann et al. 2002). Environmental concentrations of many of the most commonly used pesticides are not high enough to cause direct mortality (Fellers et al. *in press*). However, chlorpyrifos, diazinon, and malathion breakdown products increase in toxicity to native anurans with longer term exposures (Sparling and Fellers, 2007, 2009).

Linking the potential interaction between environmental contaminants and disease has been difficult. However, a recent study has shown that early life exposure to the herbicide atrazine had enduring effects on pathogen-

Table 6. Estimated parameter values for occupancy models for each species. Elevation, pond depth, and shore length covariates were all standardized to have a mean of 0 and SD of 1 so effect sizes are consistent with a 1 SD change in the covariate on the logit scale. Ψ_0 = the initial probability a site is occupied, γ = the probability an unoccupied site was occupied in the following year, ϵ = the probability an occupied site was unoccupied in the following year. Basin was coded as Tuolumne = 1 and Merced = 0; negative values indicate lower occupancy in the Tuolumne basin. Fish presence was coded as 1 = present and 0 = not present; negative values indicate that anuran occupancy was lower where fish were present. Sensitivities ($\Delta\Psi_0/\Delta X$) measure the relative rate of change in predicted equilibrium occupancy as the value of continuous covariates are increased (Miller 2012). Larger sensitivity values indicate greater long-term effects on occupancy, and the sign tells the direction of that effect.

	Ψ_0	γ	ϵ	$\Delta\Psi_0/\Delta X$
Any Life Stage				
<i>Rana sierrae</i>				
basin	-0.23 (0.22)	-1.05 (0.43)	-0.11 (0.30)	--
fish	-0.79 (0.27)	-0.03 (0.38)	0.15 (0.46)	--
elevation	-0.59 (0.23)	-1.60 (0.40)	-0.79 (0.35)	-0.14
maximum depth	0.88 (0.21)	0.60 (0.30)	-0.28 (0.35)	0.14
shore length	0.47 (0.23)	-1.70 (0.89)	-1.69 (0.67)	-0.02
<i>Anaxyrus canorus</i>				
basin	-0.03 (0.32)	-0.97 (0.49)	1.25 (0.84)	--
elevation	0.88 (0.28)	1.02 (0.43)	2.08 (0.90)	0.21
elevation ²	0.70 (0.19)	0.52 (0.57)	-0.97 (0.48)	--
maximum depth	-0.76 (0.31)	-1.14 (0.63)	0.15 (0.66)	-0.08
shore length	0.20 (0.24)	0.57 (0.28)	-0.51 (0.54)	0.06
<i>Pseudacris regilla</i>				
fish	-0.65 (0.18)	-0.24 (0.18)	-0.23 (0.19)	--
elevation	0.05 (0.21)	-0.02 (0.21)	0.20 (0.15)	-0.05
maximum depth	0.58 (0.20)	-0.45 (0.19)	0.06 (0.15)	-0.09
Reproductive Stages				
<i>Rana sierrae</i>				
basin	0.13 (0.26)	-0.90 (0.42)	-0.75 (0.56)	--
fish	-7.44 (***)	-8.86 (***)	11.44 (***)	--
elevation	0.05 (0.26)	-1.31 (0.41)	-0.66 (0.41)	0.00
maximum depth	0.65 (0.24)	0.93 (0.32)	-1.03 (0.59)	0.00
shore length	0.61 (0.26)	0.86 (0.29)	-1.57 (0.81)	0.00
<i>Anaxyrus canorus</i>				
basin	0.61 (0.45)	-0.64 (0.33)	0.27 (0.95)	--
fish	0.63 (0.27)	-0.36 (0.31)	-0.05 (0.30)	--
elevation	0.36 (0.32)	0.30 (0.29)	0.70 (0.79)	0.01
elevation ²	0.57 (0.21)	0.12 (0.23)	-0.07 (0.37)	--
maximum depth	-0.45 (0.36)	-1.55 (0.47)	0.42 (0.37)	-0.14
shore length	0.17 (0.32)	0.84 (0.27)	-0.30 (0.34)	0.08
<i>Pseudacris regilla</i>				
fish	-0.83 (0.24)	-0.06 (0.17)	-0.27 (0.28)	--
elevation	-0.15 (0.20)	0.14 (0.22)	-0.13 (0.22)	-0.05
elevation ²	-0.31 (0.16)	-0.23 (0.20)	-0.06 (0.18)	--
maximum depth	0.30 (0.20)	0.14 (0.17)	0.51 (0.18)	-0.08
shore length	0.07 (0.21)	-0.44 (0.26)	-0.46 (0.28)	0.01

*** No evidence of reproduction for *R. sierrae* was found in any pond known to contain fish. We could not calculate sampling error for resulting estimates because they occurred at the boundary of 0.

induced (amphibian chytrid) mortality in Cuban treefrog (*Osteopilus septentrionalis*) larvae (Rohr et al. 2013). While atrazine is the most widely used herbicide in the U.S., there is little or no atrazine exposure in the Sierra Nevada, but a wide range of other insecticides, fungicides and pesticides are used just upwind of Yosemite N.P. and many of these compounds are present at amphibian breeding sites in the Sierra Nevada (Smalling et al. 2013; Fellers et al. *in press*). Additional studies are needed to better understand the interaction between multiple stressors and their role in amphibian declines.

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APPENDIX

Table S1. We considered the following set of alternative models for each combination of species and life stage (any life stage versus reproductive stages) to evaluate their influence on detectability and occupancy. We included a categorical effect of year on extinction and colonization in all occupancy parameter models.

Detection Models

- 1 - year
- 2 - observer and date
- 3 - year, and temp
- 4 - observer, date, and temp

Occupancy Models (ψ_0 , ϵt , and γt).

- 1 - basin, elevation², maximum depth, shore length, fish
- 2 - basin, elevation², maximum depth, fish
- 3 - basin, elevation², shore length, fish
- 4 - basin, elevation², fish
- 5 - basin, elevation, maximum depth, shore length, fish
- 6 - basin, elevation, maximum depth, fish
- 7 - basin, elevation, shore length, fish
- 8 - basin, elevation, fish
- 9 - elevation², maximum depth, shore length, fish
- 10 - elevation², maximum depth, fish
- 11 - elevation², shore length, fish
- 12 - elevation², fish

- 13 - elevation, maximum depth, shore length, fish
- 14 - elevation, maximum depth, fish
- 15 - elevation, shore length, fish
- 16 - elevation, fish
- 17 - basin, elevation², maximum depth, shore
- 18 - basin, elevation², maximum depth
- 19 - basin, elevation², shore
- 20 - basin, elevation²
- 21 - basin, elevation, maximum depth, shore
- 22 - basin, elevation, maximum depth
- 23 - basin, elevation, shore
- 24 - basin, elevation
- 25 - elevation², maximum depth, shore
- 26 - elevation², maximum depth
- 27 - elevation², shore
- 28 - elevation²
- 29 - elevation, maximum depth, shore
- 30 - elevation, maximum depth
- 31 - elevation, shore
- 32 - elevation