
ADVANTAGES OF LONG-TERM, MULTI-SCALE MONITORING: ASSESSING THE CURRENT STATUS OF THE YOSEMITE TOAD (*ANAXYRUS [BUFO] CANORUS*) IN THE SIERRA NEVADA, CALIFORNIA, USA

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Abstract.—A comprehensive bioregional evaluation of the current status of at-risk species is critical for effective management and conservation. As part of a long-term, multi-scale amphibian monitoring program, we evaluated the current status of the Yosemite Toad (*Anaxyrus [Bufo] canorus*) on national forest lands across the species' range in the Sierra Nevada, California, USA. We conducted monitoring at extensive (rangewide) and intensive (individual population) scales with small watersheds (2–4 km²), individual meadows, and breeding areas within meadows as sample units. Yosemite Toad breeding was found in an estimated proportion of 0.84 ± 0.03 (SE) of recently occupied watersheds (locality data from 1990–2001), and 0.13 ± 0.04 of historically occupied watersheds (locality data prior to 1990). Rangewide, breeding was found in an estimated proportion of 0.22 ± 0.01 of watersheds. We quantified demographic parameters (abundance and survival of breeding males, abundance of egg masses, successful metamorphosis) in six meadows in two watersheds. Abundances were small, with the largest populations having only 16–21 and 18–19 breeding males each year. Annual survival rates of males by meadow ranged from 0.49–0.72. Numbers of egg masses per year were low, and the proportion of breeding areas with successful metamorphosis ranged from 0.14–0.73. Using the multi-scale data, we examined Yosemite Toad spatial and temporal occupancy patterns. Yosemite Toads tended to breed in one or two sites (lakes, meadows, stream reaches) per watershed every year, and occasionally in other sites. This assessment of the status of the Yosemite Toad will inform management decisions at both bioregional and population scales and the development of conservation priorities.

Key Words.—amphibian demography; *Anaxyrus canorus*; bioregional monitoring; multi-scale monitoring; Sierra Nevada; Yosemite Toad

INTRODUCTION

Amphibians are imperiled worldwide (Beebee and Griffiths 2005; Wake and Vredenburg 2008) and over 40% of all amphibian species have decreasing population sizes (Stuart et al. 2004). As efforts to identify and monitor at-risk populations have increased, the role of spatial and temporal scale in providing robust assessments of status and understanding the population dynamics of amphibians has come to the forefront (Hecnar and M'Closkey 1997; Meyer et al. 1998; Skelly et al. 2003). Many population studies have been conducted at local scales such as individual lakes or ponds and often over short time periods (Briggs and Storm 1970; Pechmann et al. 1991; Richter and Siegel 2002). However, bioregional assessments, generally conducted over large areas often defined by ecological characteristics, are needed to fully evaluate a species status (Stuart et al. 2004; Gompper and Hackett 2005; Bonardi et al. 2011; Cameron et al. 2011; Gould et al. 2012), and monitoring over broader spatial and temporal scales may be more effective at separating general population trends from local fluctuations (Pechmann et

al. 1991; Hecnar and M'Closkey 1997; Meyer et al. 1998; Skelly et al. 2003; Trenham et al. 2003). Logistically, the types of data that are feasible to collect at bioregional and local scales differ (see Beebee and Griffiths 2005). Detailed abundance and demographic data provide the most insight into population dynamics, but are usually too expensive and logistically impractical to collect long-term and over large geographic areas. As a result, researchers increasingly use occupancy data as a more cost-effective alternative (Trenham et al. 2003; Bailey et al. 2004; Corn et al. 2005; Gould et al. 2012). However, occupancy data alone provide no information on changes in abundance, which may be a first sign of impending distributional declines (Muths et al. 2003; Weir et al. 2009; Collen et al. 2011), or key vital rates and life-stage specific population dynamics (Berven 1990; Semlitsch et al. 1996; Biek et al. 2002; Scherer et al. 2005). One solution is to collect occurrence data across bioregional scales to evaluate rangewide persistence and more detailed demographic data at a smaller subset of locations to provide insights on local population dynamics such as abundance, survival, and recruitment (e.g., Corn et al. 1997).

The Yosemite Toad (*Anaxyrus [Bufo] canorus*) is a species well suited for a multi-scaled monitoring approach. The Yosemite Toad is endemic to the Sierra Nevada, California, where it occurs predominantly on public lands (almost 99% of its range), much of which is in wilderness areas. Declines in the Yosemite Toad have been documented (Kagarise Sherman and Morton 1993; Jennings and Hayes 1994; Drost and Fellers 1996), and the U.S. Fish and Wildlife Service has determined that listing the species as endangered under the Endangered Species Act is warranted but precluded by higher priority actions (U.S. Fish and Wildlife Service 2002). However, a comprehensive assessment of status across the species' range has not previously occurred and potential causes of decline are not well understood.

There are multiple challenges to monitoring the Yosemite Toad. If surveys are timed correctly, all life stages are relatively easy to detect; however, the suitable survey periods for each life stage are relatively short and are not concurrent. Breeding commonly occurs in shallow, warm water areas that typically dry over the summer and include wet meadows, shallow ponds, shallow flooded, grassy areas adjacent to lakes, and slow flowing streams (Karlstrom 1962). Yosemite Toads are explosive breeders where adults arrive at snowmelt, lay eggs over a short period of time, and then leave the breeding areas (Kagarise Sherman 1980). Because they are not commonly found after breeding, surveys for adults must occur at snowmelt over a 1–2 week period, when most locations are difficult to access. Eggs hatch into larvae in about 4–15 days (Karlstrom 1962; Kagarise Sherman 1980), tadpoles often metamorphose by early to mid August (Karlstrom 1962; pers. obs.), and metamorphs disperse from immediate breeding areas (pers. obs.). The rapid development, desiccation of ephemeral breeding areas, and dispersal behavior result in a short survey window for each of these stages, which, combined with the remote locations of much of the species' range, makes it logistically difficult to collect demographic information on all life stages over bioregional scales.

To provide a comprehensive bioregional assessment of the status of the Yosemite Toad that addressed these monitoring challenges, the USDA Forest Service implemented a long-term multi-scale monitoring program on national forest lands in the Sierra Nevada. In an extensive component, we estimated the proportion of occupied watersheds at the scale of the range of the Yosemite Toad on national forest lands using a spatially balanced, unequal probability survey design. In an intensive component, we estimated abundance and survival of adult breeding males, number of egg masses, and successful metamorphosis in six meadows in two watersheds. Between the two components, we conducted surveys at three scales, watershed, site (lake, meadow, stream reach), and breeding area (contiguous

lentic water) within sites. In this paper, we present a baseline assessment of bioregional population status for the Yosemite Toad. We also show how data collected for status and trend can be used to address other questions useful for management by presenting insights on Yosemite Toad spatial and temporal occupancy patterns.

MATERIALS AND METHODS

Study region.—The study region for the extensive component is the portion of the historical range of the Yosemite Toad that occurs on national forest lands within the Sierra Nevada, California, USA (Fig. 1). This area comprises about 10,500 km² extending from Alpine County south to Fresno County and contains survey watersheds at elevations from 1,859 to 3,703 m. Aquatic habitats within the study region are chiefly fed by snowmelt, and include lakes, ponds, wet meadows, and streams, which vary greatly in size, vegetation, hydrology, and topography. A variety of management activities occur within the study region although much is in designated wilderness where management activities are more limited and access is only by foot or pack animal. Livestock grazing occurs in many Sierran meadows and legacy effects exist even in those areas where grazing no longer occurs (Menke et al. 1996). Fish stocking has occurred since the late 1800's and is still widespread (Bahls 1992; Knapp 1996), and recreational activities are increasing in high elevation wilderness areas (USDA Forest Service 2001). Other activities such as vegetation, fire and fuels, and road management also may affect the species at lower elevations.

The two intensive watersheds included Bull Creek (4.86 km²), located in Fresno County in the southern Sierra Nevada, and Highland Lakes (2.9 km²), located in Alpine County in the central Sierra Nevada (Fig. 1). Elevations in Bull Creek range from 2,134 m to 2,489 m and vegetation is predominantly forested with small meadow and riparian openings (0.33 ha to 5.1 ha). Management activities occurring in the watershed include livestock grazing, recreation, timber harvest, and ongoing ecological research. Highland Lakes, situated in a saddle surrounded by high peaks, is chiefly open with large areas of alpine meadow containing numerous small pools and areas of flooded vegetation. Elevations of suitable Yosemite Toad habitat range between 2,536 m and 2,621 m. This watershed contains a popular campground and draws large numbers of visitors for both summer and winter recreational activities. Livestock grazing also occurs in the watershed.

Design and field methods extensive component.—Probability-based survey designs such as the one used in this program require a precisely defined target

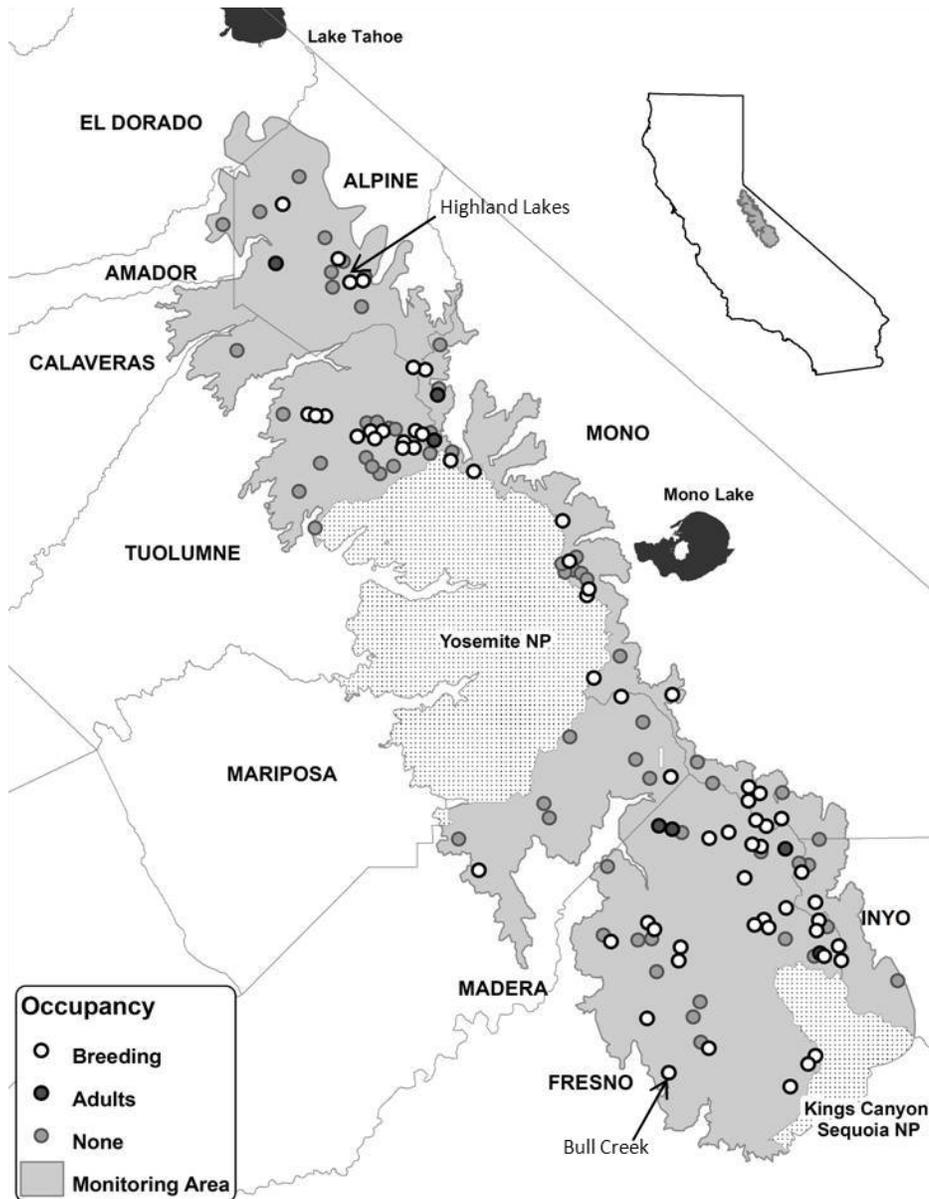


FIGURE 1. Study region and distribution of known occupied watersheds for the Yosemite Toad (*Anaryxus canorus*) in the Sierra Nevada, California, USA. The monitoring area is national forest lands within the range of the Yosemite Toad. Bull Creek and Highland Lakes are the two Yosemite Toad intensive watersheds

population (i.e., the set of units defining the geographic scope of inference) and a sample frame (commonly a geographic information system [GIS] representation of the target population) from which the sample is selected (Olsen et al. 1999). We defined our target population as all watersheds, delineated to 2–4 km² in size, with available aquatic habitat on national forest lands within the range of the Yosemite Toad. Because there was no existing sample frame (e.g., GIS coverage) and it was

not feasible to create one (i.e., delineate all 2–4 km² watersheds within the monitoring area), we used the Forest Inventory and Assessment (FIA) systematic random hexagonal grid (Brand et al. 2000) densified to hexagons of 2.6 km².

We compiled all available Yosemite Toad locality data from state and federal agency records, academic researchers, and from literature and museum sources. We assigned each of the 10,077 hexagons (and

corresponding grid point centers) in the sample frame to one of three mutually exclusive temporal categories based on the compiled locality data: (1) *Recent*, toads documented within 10 years prior to the start of the sampling (defined to be after 1990); (2) *Historical*, toads documented only prior to 1990; and (3) *Unknown*, no locality data. A spatially distributed random sample was selected from the sample frame using a generalized random tessellation stratified survey design (GRTS) for a finite resource with unequal probability of selection based on the three temporal categories (Stevens and Olsen 1999; Stevens and Olsen 2004). We selected a larger proportion of the sampled hexagons from areas most likely to have Yosemite Toads (*Recent*). We delineated watersheds, 2–4 km², around the selected grid point centers using the Hydrologic Unit Code rule set (U.S. Department of Agriculture 1997).

Temporally, the study design uses an augmented serially alternating panel design (Urquhart et al. 1998; Urquhart and Kincaid 1999). The initial design specified that 20% of the *Recent* watersheds ($n = 16$) were to be visited every year (referred to as the annual watersheds), and the remaining watersheds once every five years on a rotating schedule. Due to funding limitations, the full sample of watersheds took eight years to complete (2002–2009). Based on preliminary analyses of the first five years of data, we determined that completing the full sample, thereby increasing the precision of the estimates, was more important than beginning the second cycle.

We determined watershed occupancy by surveys of all lentic (lakes, wet meadows) and a sample of lotic habitat (perennial and ephemeral streams) within each watershed. We identified lakes and meadows using aerial photographs that we verified in the field. We randomly selected three 300-m perennial stream reaches per watershed, one from each of three gradient classes (low < 2%, medium 2–8%, and high > 8%), and two 100-m ephemeral stream reaches located in meadows from a USDA Forest Service Sierra-wide GIS coverage (Region 5 Remote Sensing Lab in 2001, available from Cathy Brown). We refer to the individual lakes, meadows, and selected stream reaches in each extensive watershed as sites.

From June–September 2002–2009, we used Visual Encounter Surveys (VES) to determine Yosemite Toad occupancy in each extensive watershed (Crump and Scott 1994; Olson et al. 1997). We surveyed all wadeable water at each site (lake, meadow, and selected stream reach) and we made an effort to survey watersheds early in the season before sites dried up to maximize detection of the tadpole stage. Although our primary goal was to detect tadpoles, we recorded data on all life stages observed.

Design and field methods intensive component.—We subjectively selected two intensive watersheds using the following criteria: (1) contained a variety of aquatic habitat types; (2) contained at least three breeding lakes, meadows, or stream reaches separated by more than 200 m; (3) supported a relatively large number of adult toads; and (4) had easy access at snowmelt and during the summer. From 2006–2009, we visited three meadows in each watershed at snowmelt to conduct adult capture-mark-recapture (CMR) and egg mass surveys (Bull Creek meadows: 520M15, 520M16, 520M20; Highland Lakes meadows: 37188, 37213, 37165). The ecology of the Yosemite Toad is ideal for using Pollock's robust design (Pollock 1982; Kendall et al. 1997) to estimate abundances of breeding males during their spring chorus. The robust design is two-tiered with primary sampling periods that occur over longer intervals that allow population gains (recruitment/immigration) and losses (mortality/emigration), and secondary sampling occasions within each primary period where the population is assumed to be closed. We treated each annual breeding period as a primary sampling period. Because males congregate in breeding choruses for the short duration of the breeding period, we treated multiple samples over consecutive days during each primary period as secondary occasions from a population that is relatively closed. The robust design is not as suitable for estimating female abundances. Female toads remain in breeding areas for only a few days leaving shortly after amplexus, thus violating the assumption of population closure among the secondary occasions. Still, we marked females when possible.

We conducted CMR surveys as soon as breeding choruses formed at snowmelt and surveys continued for at least five consecutive days each year. The timing of snowmelt and the subsequent breeding varied among years ranging from late April to mid May in Bull Creek and from late May to late June at Highland Lakes. We surveyed each intensive meadow for at least six hours each day. At each meadow, crews rotated among the breeding choruses, visually scanning the breeding areas, actively searching in burrows and under ground cover, and using cues from calling males to locate toads. All unmarked toads > 40 mm snout-urostyle length (SUL) were PIT-tagged (passive integrated transponder; Martin 2008) using AVID MUSICC Microchips™ (Avid Identification Systems, Inc., Norco, California, USA) and released. Upon initial capture each year, we recorded the snout-urostyle length, weight, and sex of each toad. We identified marked animals by their unique tag numbers at each subsequent recapture, and we used these data to create capture histories.

We conducted egg mass counts at the end of the five day adult CMR period. Conducting counts of Yosemite Toad egg masses can be challenging because females lay eggs in long strings and sometimes split masses over two

or more locations or lay them communally. Also, eggs may hatch prior to the completion of the five day period or be deposited after counts are conducted. To address these challenges, we used several methods to determine the most efficient approach. We used the more intensive dependent double-observer method (Grant et al. 2005) in 2006 and independent double-observer method (Nichols et al. 2000) in 2007 and 2008. After employing and testing these multiple observer methods, individual egg mass detection probabilities were very high (> 0.96) and consistent among observers. Accordingly, in 2009 we simply used a tally of unique eggs masses (i.e., conditional probability of detection = 1) from a single observer. This was simpler and more efficient, and in our judgment, an accurate estimate of the number of Yosemite Toad masses laid each year. Although the methods differed among years, the estimates of egg mass numbers were similar and reasonable given the numbers of adults we observed. Thus, in our judgment, the three methods were comparable. In addition, based on our observations during the five day period and our subsequent surveys of these meadows for the extensive component, it is unlikely that we missed large numbers of egg masses.

In 2006, we visited each intensive meadow every two weeks (Bull Creek 29 June - 25 August; Highland Lakes 12 July - 7 September) for a total of six visits. At each breeding area in each intensive meadow, two observers independently counted tadpoles and metamorphs. Additional surveys were conducted by one observer at Bull Creek once per week (10 visits, 17 June - 19 August) in 2009 and at Highland Lakes once every two weeks (five visits, 15 June - 27 August) in 2007 and twice (14 July, 29 July) in 2008. These data were used to document successful metamorphosis for each breeding area.

Analysis extensive component.—We based the analyses of occurrence data on an unequal probability survey design where the weight for each watershed evaluated is the inverse of the probability of selection for that watershed (Diaz-Ramos et al. 1996). The contribution of each sample watershed to the final estimate is proportional to the watershed weight. For example, sample watersheds with higher probability of selection (e.g., *Recent* watersheds) have lower weights and thus contribute less to the final estimate. We conducted analyses using the R software (R Development Core Team, Vienna, Austria), an R contributed library (spsurvey: Spatial Survey Design and Analysis, Kincaid and Olsen 2009) developed for the statistical analysis of probability survey data, and SAS® software (SAS Institute Inc., Cary, North Carolina, USA).

The presence of tadpoles indicates the existence of a reproducing population rather than, for example, an adult

moving through an area. Therefore, our primary goal was to estimate the proportion of watersheds occupied (ψ) by breeding (eggs, tadpoles, or metamorphs). Too few adults were found to model them separately, so to account for all areas occupied by the species, we also estimated the proportion of watersheds occupied by any life stage. For both occupancy states (breeding, any life stage), we estimated the proportion of occupied watersheds for the entire range of the species (rangewide, $\psi(\cdot)$) and relative to the temporal period when toads were last observed (*Recent*, *Historical*, *Unknown*, $\psi(\text{temporal category})$). We used a maximum likelihood approach that incorporates the probability of detecting the species (p) and the watershed weights (described below; also MacKenzie et al. 2006). Methods that do not account for p typically result in an underestimate of occupancy unless the probability of detection is near one (MacKenzie et al. 2006). We assumed that the occurrence of toads was closed during the eight-year monitoring period (i.e., occupancy state in each watershed did not change) and used the annual watershed data to estimate the probability of detection. This approach differs from most studies where visits occur over shorter time periods, typically within a season. If the population closure assumption is violated, the probability of occupancy may be overestimated. We recognize that eight years may be a long time to assume that watershed occupancy is constant. Our approach may be reasonable given the likely slow and persistent effects resulting from many management activities, but be more questionable for threats such as an epidemic pathogen that causes widespread and rapid declines. We address this assumption and its implications in our discussion.

We modeled p as a function of two covariates, survey date (measured by the number of days from January 1) and snow pack of the preceding winter. Snowpack was quantified as the percentage of normal snowpack for the Sierra Nevada measured on 1 April each year (California Department of Water Resources, California Data Exchange Center. Available from <http://cdec.water.ca.gov/> [Accessed 17 September 2009]). The Sierra Nevada receives most of its precipitation between December and April (Howat and Tulaczyk 2005). Date of survey and seasonal water are important factors for detecting many amphibian species (Schmidt 2005; Weir et al. 2005; Lacan et al. 2008). Yosemite Toads breed in ephemeral habitats and metamorphose within one summer. Thus, we predicted that p should be highest in early season surveys and in years with higher snow pack (i.e., more available water). Habitats dry up sooner in drought years, so we tested for a survey date and snow pack interaction. We developed ten a priori models where ψ = probability of occupancy and p = probability of detection (Table 1).

We used a generalized version of the maximum

TABLE 1. Model selection for occupancy estimates for the Yosemite Toad (*Anaryxus canorus*) for breeding and any stage, summarized rangewide and by temporal category. K is the number of parameters in the model. AIC_c is the Akaike Information Criterion adjusted for small sample sizes. w_i is the Akaike weight for comparing models. ψ is the probability of occupancy and p is the probability of detection. Models comprising $\geq 95\%$ of the weight are in bold.

Breeding					Any Stage				
Model	K	AIC_c	ΔAIC_c	w_i	Model	K	AIC_c	ΔAIC_c	w_i
Rangewide, ψ (.)									
p(Survey Date * Snow Pack)	5	1851.7	0.0	0.996	p(Survey Date * Snow Pack)	5	2059.9	0.0	1.000
p (Snow Pack)	3	1862.8	11.1	0.004	p (Survey Date + Snow Pack)	4	2232.0	172.2	0.000
p (Survey Date + Snow Pack)	4	1885.2	33.5	0.000	p (Snow Pack)	3	2276.0	216.2	0.000
p (.)	2	2027.4	175.7	0.000	p (Survey Date)	3	2368.6	308.8	0.000
p (Survey Date)	3	2029.3	177.6	0.000	p (.)	2	2372.0	312.2	0.000
Temporal Category, ψ (Temporal Category)									
p(Survey Date * Snow Pack)	7	1459.8	0.0	1.000	p(Survey Date + Snow Pack)	6	1872.7	0.0	1.000
p (Snow Pack)	5	1487.8	28.0	0.000	p (Snow Pack)	5	1909.8	37.2	0.000
p (Survey Date + Snow Pack)	6	1523.4	63.6	0.000	p (Survey Date * Snow Pack)	7	1913.8	41.2	0.000
p (.)	4	1534.1	74.3	0.000	p (.)	4	1955.4	82.7	0.000
p (Survey Date)	5	1538.6	78.8	0.000	p (Survey Date)	5	1957.6	85.0	0.000

likelihood procedure developed by MacKenzie et al. (2002) appropriate for our more complex unequal probability survey design. The following notation is used: S, the number of space-time subunits in the study; n_s , the number of watersheds in the sample in subunit s; V, number of distinct seasonal sampling occasions; ψ_{si} , probability that a species is present in watershed i within subunit s; p_{siv} , probability of detecting a species in watershed i within subunit s on visit v, given the species is present. Then let $\mathbf{d}_{si} = (d_{si1}, d_{si2}, \dots, d_{siv})$ where

$$d_{siv} = \begin{cases} 1 & \text{if species is detected in watershed } i \text{ in} \\ & \text{subunit } s \text{ on visit } v \\ 0 & \text{if species is not detected in watershed} \\ & \text{ } i \text{ in subunit } s \text{ on visit } v \\ \text{NA} & \text{if no visit was made in watershed } i \text{ in} \\ & \text{subunit } s \text{ on visit } v \end{cases}$$

and $s=1, \dots, S$, $i=1, \dots, n_s$ and $v=1, \dots, V$. Let $\mathbf{x}_{si} = (x_{si1}, x_{si2}, \dots, x_{siK})$ be K watershed-specific covariates for watershed i within subunit s and

$$\mathbf{y}_{si} = \begin{bmatrix} y_{si11} & \dots & y_{siV1} \\ \vdots & \ddots & \vdots \\ y_{si1M} & \dots & y_{siVM} \end{bmatrix}$$

be M watershed-specific and visit-specific covariates for watershed i within subunit s. The likelihood equation for a stratified unequal probability survey design, such as the one used in this program, is

$$L(\boldsymbol{\Psi}, \mathbf{p} | \mathbf{x}, \mathbf{y}, \mathbf{d}) = \prod_{s=1}^S \prod_{i=1}^{n_s} f(\mathbf{d}_{si} | \mathbf{x}_{si}, \mathbf{y}_{si})^{w_{si}}$$

$$= \prod_{s=1}^S \prod_{i=1}^{n_s} \left[\prod_{v=1}^V \left((1 - p_{siv})^{(1-d_{siv})} p_{siv}^{d_{siv}} + D(\mathbf{d}_{si}) \right) \right]^{w_{si}}$$

where S subunits are present and each watershed has a weight, w_{si} , and

$$D(\mathbf{d}_{si}) = \begin{cases} 0 & \text{if } \mathbf{1}'\mathbf{d}_{si} > 0 \\ 1 - \psi_{si} & \text{if } \mathbf{1}'\mathbf{d}_{si} = 0 \end{cases}$$

and both ψ_{si} and p_{siv} may depend on the covariates. The term $D(\mathbf{d}_{si})$ distinguishes the watersheds where a species is detected on at least one visit and those sites where a species is not detected on any visits. This is the same likelihood equation as in MacKenzie et al. (2002) when all weights are equal, as is the case for a simple random sample. We maximize the log likelihood using the function “optim” in R (R Development Core Team, Vienna, Austria). Variance estimates for ψ and p are obtained from the Fisher information matrix derived from the Hessian matrix evaluated at the ψ and p estimates. Confidence intervals are constructed as the estimate \pm the square root of these variance estimates multiplied by the $(1 - \alpha/2)$ th percentile of the standard normal distribution. We evaluated the relative support for each model using Akaike Information Criterion for small sample sizes (AIC_c) and Akaike weights (w_i) (Burnham and Anderson 2002). We dropped models that could not be fit to the data from the model set and we used the remaining models to compute model-averaged estimates (Burnham and Anderson 2002; MacKenzie et al. 2006).

Analysis intensive component.—We analyzed capture history data for male Yosemite Toads to estimate abundances during spring breeding and apparent annual survival rates. We designated survival “apparent”

because we cannot distinguish between male Yosemite Toads that die from those that permanently emigrate (Williams et al. 2002). We ran analyses separately for each of the six intensive meadows (three in each watershed). Because the robust design assumes that populations are closed over secondary occasions (there is no immigration or emigration), we tested for demographic closure for each intensive meadow each year. Examination of the capture histories suggested that any violation of the closure assumption likely resulted from immigration into the meadows during the primary period (i.e., males were not all present at the start of the secondary occasions but once present they tended to remain). Because sample sizes were small, to obtain better fitting models, we chose to test for immigration, but not emigration. This was done by fitting a Pradel model (Pradel 1996) with no immigration (recruitment = 0, closed model) and a model allowing immigration (recruitment unconstrained, open model, Boulanger et al. 2002). We compared the closed and open models for each meadow and year using likelihood ratio tests. For meadows where the closure test suggested that populations were not closed, we pooled captures from all but the last visit within each primary period such that each primary period included two secondary occasions (Kendall 1999). For meadows where populations were closed, to reduce the number of models for comparison, we conducted exploratory analysis for each meadow each year by fitting the data to four Huggins closed population models where the probability of capture was held constant (M_o) or allowed to vary by behavior (M_b), time (M_t), or both (M_{tb}) (White et al. 1982). For each meadow, we chose the closed population model that had the most support, based on Akaike weights (w_i) using $QAIC_c$ values, for inclusion in the robust design analysis.

We fit the resulting data to four Pollock's robust design models where apparent survival (Φ) was held constant or allowed to vary among years, and the probability of capture (p) and recapture (c) were modeled with the best supported closed population model, and held constant ($p(\cdot)$), or allowed to vary among years, ($p(t)$) (Table 2). We did not include temporary emigration because in our preliminary analysis, most models could not be fit to the data or had little support, likely due to small sample sizes and the short study duration (four years). Instead, we compiled the breeding schedules of adult males from the CMR data. We used the program RDSurviv (Kendall and Hines 1999) to test the goodness of fit for the most general model for each meadow and calculate the variance inflation factor, \hat{c} , based on the Pearson's X^2 test ($\hat{c} = X^2/df$, Amstrup et al. 2005). We based model selection on Akaike weights (w_i) calculated from $QAIC_c$ values (Burnham and Anderson 2002). We calculated abundance and apparent survival estimates by model averaging of the final model set (Burnham and Anderson

TABLE 2. Final models and Akaike weights used to estimate numbers of Yosemite Toad (*Anaryxus canorus*) adult males using the robust design from 2006–2009 in six meadows in two watersheds in the Sierra Nevada, California. Models that could not be fit to the data are not included. $QAIC_c$ is the Akaike Information Criterion adjusted for small sample sizes and overdispersion. w_i is the Akaike weight for comparing models. ϕ is annual survival rate, p is probability of capture, and c is probability of recapture.

Model	# Param.	$QAIC_c$	w_i
Bull Creek Watershed			
520M16			
$\phi(\cdot)p(\cdot)c(\cdot)$	3	269.0	0.538
$\phi(\cdot)p(\text{year})c(\text{year})$	9	269.9	0.343
$\phi(\text{year})p(\cdot)c(\cdot)$	5	273.2	0.066
$\phi(\text{year})p(\text{year})c(\text{year})$	11	273.7	0.053
520M15			
$\phi(\cdot)p(\text{year})$	5	178.0	0.486
$\phi(\cdot)p(\cdot)$	2	179.0	0.286
$\phi(\text{year})p(\text{year})$	7	180.1	0.164
$\phi(\text{year})p(\cdot)$	4	182.0	0.064
520M20			
$\phi(\text{year})p(\cdot)$	3	67.9	0.873
$\phi(\cdot)p(\text{year})$	4	73.0	0.068
$\phi(\text{year})p(\text{year})$	5	73.3	0.059
Highland Lakes Watershed			
37188			
$\phi(\cdot)p(\cdot)$	2	125.5	0.516
$\phi(\cdot)p(\text{year})$	5	126.2	0.377
$\phi(\text{year})p(\cdot)$	4	129.7	0.065
$\phi(\text{year})p(\text{year})$	7	130.5	0.043
37213			
$\phi(\cdot)p(\cdot)$	2	65.0	0.670
$\phi(\text{year})p(\cdot)$	3	67.2	0.220
$\phi(\cdot)p(\text{year})$	4	69.1	0.085
$\phi(\text{year})p(\text{year})$	5	71.5	0.025
37165			
$\phi(\cdot)p(\cdot)c(\cdot)$	3	116.5	0.668
$\phi(\text{year})p(\cdot)c(\cdot)$	4	118.1	0.305
$\phi(\cdot)p(\text{year})c(\text{year})$	7	123.5	0.020
$\phi(\text{year})p(\text{year})c(\text{year})$	8	125.7	0.007

2002). We used the R (R Development Core Team, Vienna, Austria) package, RMARK (Laake, J., Version 1.9.6) for model fitting and averaging.

For years where we estimated egg mass abundances, via either the double observer or independent double observer methods, we analyzed the data using the program DOBSERV (Hines, J.E., U.S. Geological Survey, Laurel, Maryland, USA). Two models were fit to the data, $p(\cdot)$ and $p(\text{observer})$, where the probability of detection was held constant and allowed to vary among

observers, respectively. Finally, for each year and watershed, we calculated the proportion of breeding areas where metamorphs were detected.

Analysis of spatial and temporal occupancy patterns.—We examined temporal and spatial breeding occupancy patterns at three scales: watershed (extensive component), site (individual lake, meadow, or stream reach in the extensive watersheds), and breeding area (contiguous areas of standing water) in the intensive meadows. In this analysis, we included only the annual watersheds where breeding occupancy was detected in at least one survey ($n = 14$ watersheds) and the intensive meadows. Because of the small sample size, our objective of examining temporal and spatial patterns together, and the fact that we did not have multiple surveys within a year to estimate probability of detection, we chose a descriptive approach rather than more complex dynamic occupancy modeling (e.g., MacKenzie et al. 2003). This descriptive approach does not incorporate probability of detection. To examine temporal variability, we assigned watersheds, sites, and breeding areas to one of three categories: (1) occupied every year surveyed; (2) unoccupied only one year; and (3) unoccupied 2+ years. We also examined both temporal and spatial occupancy in combination by looking at the number of sites per extensive watershed and breeding areas per intensive meadow that were consistently occupied by breeding. We defined consistently occupied to be occupied every year or unoccupied only one year. We assigned watersheds and intensive meadows to three categories: (1) three or more sites/breeding areas consistently occupied every year; (2) only one or two sites/breeding areas consistently occupied every year; and (3) no sites/breeding areas consistently occupied every year.

RESULTS

Extensive component.—Within the range of the Yosemite Toad, we surveyed 134 watersheds between 2002 and 2009, including 18 that were surveyed annually (Table 3). The interaction model, $p(\text{survey date} * \text{snow pack})$, had the most weight for both breeding and any stage occupancy rangewide and for breeding occupancy by temporal category (Table 1). The best model for any stage by temporal category was $p(\text{survey date} + \text{snow pack})$. In general, these models indicated a high probability of detection (≥ 0.8) if surveys are conducted early enough in the season (e.g., prior to mid August) in all but the lowest snow pack years such as occurred in 2007 (snowpack was 45% of average on April 1).

The rangewide occupancy estimate ($\hat{\psi}$) for the Yosemite Toad was 0.22 ± 0.012 (SE) for breeding and 0.29 ± 0.013 for any stage (Table 3, Fig. 1). Breeding

TABLE 3. Sample sizes for monitoring surveys and the estimated proportion of occupied watersheds ($\hat{\psi}$) for the Yosemite Toad (*Anaryxus canorus*) from 2002–2009. $\hat{\psi}$ and the standard error (SE) are shown for breeding and any stage rangewide and by temporal category. The estimated # of watersheds is the estimated number of watersheds of the target size (2–4 km²) within the range of the species.

	Range	Recent	Historical	Unknown
# Watersheds Surveyed	134	69	20	45
# Annual Survey Watersheds	18	12	0	6
# Sites Surveyed	2213	1243	273	697
Estimated # Watersheds	3069	213	103	2753
Estimated # Watersheds SE	1415	38	64	1415
# Breeding	65	45	9	11
$\hat{\psi}$ Breeding	0.22	0.84	0.13	0.05
SE Breeding	0.012	0.032	0.038	0.004
# Any Stage	72	48	10	14
$\hat{\psi}$ Any Stage	0.29	0.85	0.15	0.08
SE Any Stage	0.013	0.031	0.042	0.005

was found in a relatively large proportion of the *Recent* watersheds ($\hat{\psi} = 0.84 \pm 0.032$) compared to only 0.13 ± 0.038 of *Historical* watersheds (those occupied prior to 1990). Finally, breeding was observed in an estimated 0.05 ± 0.004 of *Unknown* watersheds. Occupancy estimates for any stage were similar to those for breeding; adults were found in few additional watersheds that did not have breeding.

Intensive component.—The Pradel models could not be fit to the mark-recapture data for four meadow-year combinations, probably due to low sample sizes. Based on the likelihood ratio test, populations were closed in two intensive meadows and open in three intensive meadows most years surveyed; the sixth meadow could not be modeled. For the meadow-years with open populations, the parameter estimates for immigration rates were low (range = 0.06–0.26) suggesting that violation of the closure assumption was not severe. The behavior model, M_b (the probability of capture, p , differs from the probability of recapture, c), had the most support in the two intensive meadows where populations were closed (Table 2). Overall, the goodness-of-fit analysis suggested that the most general model adequately fit the data with \hat{c} values ranging from 1.0–1.8. Because there was some overdispersion, we used $QAIC_c$ for our model selection criteria and adjusted the standard errors by \hat{c} for each meadow.

The total number of unique individuals captured per intensive meadow during the four-year monitoring period ranged from 4–37 for males and 5–38 for females. Accordingly, annual population estimates were also small (Table 4). The largest populations in each watershed had estimates of only 16 (meadow 520M15 in

TABLE 4. Estimates of numbers of Yosemite Toad (*Anaryxus canorus*) breeding adult males (M), egg masses, male survival (ϕ), and counts of females (F) encountered from 2006–2009 in six meadows in two watersheds of the Sierra Nevada, California, USA. Number of individuals (# Indiv) is the number of unique male and female toads found during the four year period. Confidence intervals (CI) are 95%.

		520M15			520M16			520M20			37188			37213			37165		
		Value	SE	CI	Value	SE	CI	Value	SE	CI	Value	SE	CI	Value	SE	CI	Value	SE	CI
M	# Indiv	37			19			4			34			27			9		
	2006	20.6	1.9	19–29	13.6	4.2	11–32				19.2	1.6	18–27						
	2007	18.7	4.8	14–37	10.1	2.2	8–20	3.0	0.1	3–4	19.4	0.7	19–23	14.3	1.4	13–20	6.2	0.5	6–9
	2008	20.1	2.5	17–29	12.0	1.4	11–18	4.0	0.2	4–5	18.2	1.0	18–21	14.2	1.3	13–20	7.2	0.6	7–11
	2009	15.9	1.9	14–24	9.1	1.6	8–17	2.0	0.1	2–3	18.3	0.6	18–20	12.0	1.2	11–17	3.1	0.4	3–6
ϕ	06–07	0.64	0.12	0.39–0.83	0.69	0.12	0.44–0.87				0.71	0.08	0.53–0.85						
	07–08	0.62	0.11	0.40–0.80	0.68	0.11	0.44–0.86	0.98	0.08	0.01–0.99	0.71	0.08	0.53–0.84	0.49	0.16	0.22–0.76	0.59	0.17	0.27–0.85
	08–09	0.57	0.13	0.32–0.79	0.67	0.12	0.41–0.86	0.52	0.26	0.12–0.89	0.72	0.08	0.53–0.85	0.49	0.16	0.22–0.77	0.52	0.17	0.22–0.80
F	# Indiv.	18			15			8			38			19			5		
	2006	11			13						9			2					
	2007	4			1			6			23			11			3		
	2008	14			11			2			24			11			5		
	2009	3			6			2			26			11			0		
Eggs	2006 ¹	18	0.3	18–20	27	0.5	27–30				17	0.3	15–18	10	0.0	10–10			
	2007 ²	7	0.2	7–9	19	0.4	19–22	7	0.2	7–9	12	1.0	11–17	7	0.0	7–7	5	0.0	5–5
	2008 ²	48	7.6	40–73	28	3.1	25–39	13	0.0	13–13	20	1.3	19–26	16	0.7	16–20	5	0.0	5–5
	2009 ³	3			3			1			30			13			4		

¹Dependent Double Observer Method, ²Independent Double Observer Method, ³Number of egg masses found during surveys. Counts from this method were less influenced by difficulties distinguishing individual masses from communal masses or broken fragments.

2009) to 21 (meadow 520M15 in 2006) and 18 (meadow 37188 in 2008) to 19 (meadow 37188 in 2007) males each year. One meadow in each watershed had very small numbers (2–4 and 3–7 males, respectively) each year. The numbers of males per year was fairly consistent among years, though confidence intervals varied. Annual survival estimates for breeding males were fairly similar among meadows and among years, ranging from a low of 0.49 in meadow 37213 to a high of 0.71–0.72 in meadow 37188. Only a few toads were found in meadow 520M20 where survival was 0.98 from 2007–2008. Precision for the survival estimates was low, likely due to the small sample sizes. Of 130 unique males captured in the two watersheds, 65 (50.0%) were captured in only one year, 34 (26.2%) were captured in two years, 18 (13.8%) were captured in three years, and 13 (10%) were captured in all four years. Only six males (4.6%) were captured in nonconsecutive years.

For both the dependent and independent double observer approaches used to survey for egg masses, the constant model, $p(\cdot)$, was the best model for each intensive meadow each year and the detection probabilities were high (usually > 0.96). In general, the

numbers of egg masses were low, and within the range of the numbers of toads estimated by CMR (Table 4). In a few meadow-years, estimates were greater and had wide confidence intervals. These were in meadows and years where distinguishing individual masses from communal masses or broken fragments was particularly difficult. In general, the proportion of breeding areas with successful metamorphosis was fairly low ranging from 0.14 at Bull Creek in 2009 to 0.73 at Highland Lakes in a wet year (2006, Table 5). Although direct comparisons are possible for only one year, Highland Lakes generally had more breeding areas with successful metamorphosis than Bull Creek based both on occupancy and our general observations of numbers of metamorphs.

Spatial and temporal occupancy patterns.—At the extensive scale, 93% of the 14 watersheds surveyed annually where breeding was documented were occupied most years (Fig. 2). A single dry year, 2007, accounted for most of the documented missed breeding (four of six watersheds). The one watershed missing two years was unoccupied in 2007 and 2008. In contrast, evidence of reproduction was found most years in only 30% of

TABLE 5. Proportion of breeding areas with eggs or tadpoles that had metamorphs for the Yosemite Toad (*Anaryxus canorus*) from 2006–2009 in two watersheds in the Sierra Nevada, California.

Watershed	# Breeding Areas With Eggs or Tadpoles				# Breeding Areas With Metamorphs				Proportion of Breeding Areas with Metamorphs			
	2006	2007	2008	2009	2006	2007	2008	2009	2006	2007	2008	2009
Highland Lakes	11	7	11	9	8	3	7	*	0.73	0.43	0.64 ¹	*
Bull Creek	13	9	12	7	6	*	*	1	0.46	*	*	0.14

* No surveys were conducted to look for metamorphs.

¹Only 2 visits were made at Highland Lakes during 2008, so proportions may have been higher.

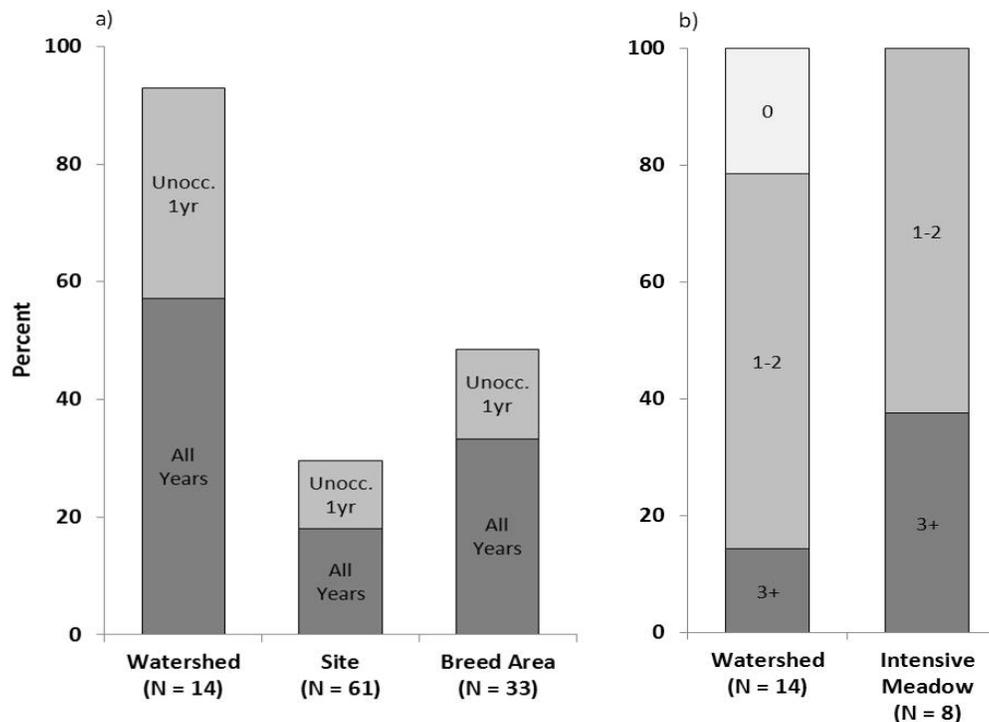


FIGURE 2. Spatial and temporal breeding occupancy patterns for the Yosemite Toad (*Anaxyrus canorus*) in the annual watersheds and intensive meadows including (a) percentage of watersheds, percentage of lakes, meadows, and stream reaches (sites), and percentage of intensive meadow breeding areas that were consistently occupied (occupied all years, unoccupied 1 year) and (b) percentage of annual survey watersheds that had 0, 1–2, or 3+ sites consistently occupied and the percentage of intensive meadows that had 0, 1–2, or 3+ breeding areas consistently occupied.

occupied sites and 49% of breeding areas (intensive meadows). The consistency in occupancy at the watershed scale supports our assumption of population closure for the occupancy estimates. Spatially, more than half of the watersheds (64%) had only one or two sites that were consistently occupied with other sites occupied only in some years (Fig. 2). Fourteen percent of the watersheds had three or more sites that were consistently occupied. Of the intensive meadows, 63% had only one or two breeding areas consistently occupied and 38% had three or more breeding areas consistently occupied. In the intensive watersheds, only three males moved among meadows during the breeding period though they did move among breeding areas within the meadows.

DISCUSSION

Based on results from this multi-scale monitoring program, we conclude that the Yosemite Toad is still fairly well-distributed but that abundances are low. Yosemite Toad occupancy has declined from levels observed historically, but toads are still fairly widespread relative to post-1990 records. Only a few assessments of Yosemite Toad occupancy have been

conducted for comparison with these monitoring results. During a 1992 resurvey of sites surveyed by Grinnell and Storer (1924), Drost and Fellers (1996) found the Yosemite Toad had disappeared or declined from 69% of the sites ($n = 13$) and that toad abundances were generally low. Jennings and Hayes (1994) found the species absent in approximately 50% ($n = 29$) of 55 historically occupied localities. No data external to the monitoring program exists to evaluate our population closure assumption for the Yosemite Toad. However, examination of occupancy in the annual watersheds indicates there has been no obvious violation within this first monitoring cycle. No trend was apparent and the pattern of detection at the watershed scale appeared to be most related to the influences of available water and survey date (Table 1, also see spatial and temporal occupancy results). Nonetheless, it is possible that our occupancy estimates are high.

Yosemite Toad abundance estimates in the two intensive watersheds were much smaller than reported historical abundances at other locations. During a long-term study at Tioga Pass Meadow, California (1971–1982), approximately 2,270 Yosemite Toads were marked with annual counts ranging from 162 to 342 males (1974–1979). In six other locations near Tioga

Pass, three Yosemite Toad populations were substantially larger and three had numbers similar to those found in our intensive meadows (Kagarise Sherman and Morton 1993). Abundances in our intensive meadows may have been substantially greater in the past. According to Martin (2008), Highland Lakes supported one of the largest breeding populations in the northern Sierra Nevada. Historical population sizes are unknown, but by the early 1980's, populations had declined to approximately 50–100 toads in one meadow in the watershed (Martin 2008). This is similar to our estimate of abundance in the entire watershed (three meadows) in a given year, suggesting that abundance has declined further since that time. The only other information on historical abundances is qualitative; historical accounts used terms such as "many males present", "common" (Grinnell and Storer 1924), and "numerous" (Mullally 1953).

If the abundances found in our intensive watersheds are reflective of a broader pattern, it may be that populations are small rangewide, even though Yosemite Toads were found to still occur in many of the *Recent* watersheds. Only $18 \pm 6.1\%$ of the occupied watersheds we surveyed rangewide had $> 1,000$ tadpoles or > 100 metamorphs, subadults, or adults detected at the time of survey (Cathy Brown, unpubl. data). Although not all surveys were conducted at the peak of tadpole presence and adults are not commonly detected outside the breeding period, these data in combination with documented local population declines (e.g., Kagarise Sherman and Morton 1993; Drost and Fellers 1996) lend support to the hypothesis that reduced abundances may be widespread in Yosemite Toad populations. Abundances of the closely related *Anaxyrus boreas* in northeastern Oregon and the Rocky Mountains of Colorado were comparable to the Yosemite Toad historical abundances from the Tioga Pass Meadow population (Muths et al. 2003; Bull and Carey 2008; Scherer et al. 2008). However, as a result of infection by the amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*), some populations in Colorado have declined to very small numbers (Muths et al. 2003; Muths et al. 2008). Whether *Bd* is a factor in Yosemite Toad declines is currently under study (Celeste Dodge, pers. comm.). *Bd* has been found in Yosemite Toads (Green and Kagarise Sherman 2001; Fellers et al. 2011) and the prevalence varies among populations and both prevalence and infection intensity is higher on juveniles than on adults (Celeste Dodge, Vance Vredenburg, Cathy Brown, and Amy Lind, unpubl. data).

No prior estimates of survival and successful metamorphosis exist for the Yosemite Toad. The apparent survival of reproductive males in our intensive meadows was similar or slightly lower than the ranges of those reported for stable populations of adult male *A. boreas* in Colorado. For example, Muths et al. (2003)

reported survival rates for *A. boreas* of 78% prior to a large *Bd* related population decline (also see Scherer et al. 2005) and Scherer et al. (2008) reported survival rates ranging from 46% to 86% in uninfected ponds. Successful metamorphosis of Yosemite Toads in our intensive meadows was generally low, particularly given that it was measured by presence rather than number of metamorphs. Reasons for the low success and apparent differences between the Bull Creek and Highland Lakes watersheds are unknown. We are in the preliminary stages of investigating these results, and at Bull Creek, our observations suggest that much of the mortality is at the egg and early tadpole development stages. This analysis would be strengthened by estimating abundances of metamorphs rather than just presence, though this is very difficult to do.

Variable and episodic reproductive success is common in aquatic amphibians suggesting that low recruitment in a given year may not necessarily reflect population declines, particularly for long-lived species like the Yosemite Toad (Berven 1990; Semlitsch et al. 1996; Taylor et al. 2006). Yosemite Toad eggs and tadpoles are susceptible to a variety of natural stochastic environmental events such as freezing and desiccation resulting in naturally high mortality and low to no recruitment in some years (Kagarise Sherman 1980; Kagarise Sherman and Morton 1993; pers. obs.). The persistence of the species over the long-term may depend on both high survival rates for the long-lived adults (15 or more years, Kagarise Sherman and Morton 1984) and periodic high recruitment (e.g., Alford and Richards 1999). This dynamic was explored by Biek et al. (2002) who found that losses of post-metamorphic life stages were more likely to lead to population declines than losses in the egg or tadpole stages. The importance of both recruitment and adult survival is demonstrated by results from long-term monitoring of an *A. boreas* population in Colorado with abundances similar to our larger Yosemite Toad populations. Persistence of the population was sustained by high rates of survival (92% for males) of long-lived adults, but recruitment was very low (2–5%), and the resulting population growth rates showed the population to be in a slow decline (Muths and Scherer 2011).

Temporal and spatial occupancy.—In the majority of our annual occupied 2–4 km² watersheds, the Yosemite Toad consistently bred in one or two lakes, meadows, or stream reaches, and then only occasionally in other sites. Similarly, in 63% of the intensive meadows, Yosemite Toads consistently bred in one or two of the breeding areas, but only occasionally in other locations (Fig. 2b). Possible explanations include (1) population sizes are too low for toads to breed every year or to saturate the available habitat; (2) toads consistently breed in the best habitat, but occasionally breed in less optimal habitat; or

(3) some sites have suitable habitat only under certain environmental conditions. For example, a site may have optimal habitat during high snowpack years but may desiccate prior to metamorphosis during low snowpack years.

Data from the intensive watersheds provided further insights on how the species uses available habitat spatially and temporally. Only a few animals moved among meadows for breeding, suggesting that Yosemite Toads have high site fidelity at the scale of individual meadows. High site fidelity is common to many toad species (Breden 1987; Sinsch 1992; Muths et al. 2006). Males did, however, move among breeding areas within the meadows. Overall, Yosemite Toads in our study appear to be selecting particular breeding areas, even though some areas were not used every year. Given the fast development of toad eggs and tadpoles, it is likely that the breeding areas are chosen based on water retention and thermal regime. The pattern of snowmelt also may play a role; areas that melt early may be chosen more often for breeding (Olson 1992; pers. obs.). Further investigation is needed to better understand these occupancy patterns including whether the sites and breeding areas that are occasionally occupied are a result of generally small population sizes or reflect habitat differences and their importance for long-term persistence.

In our intensive meadows, the proportion of toads found one, two, three, or all four years were similar to those reported by Kagarise Sherman (1980) in Tioga Pass Meadow during a 4-year period (1976–1979). Based on capture histories, only 5% of males ($n = 6$) in our intensive meadows skipped one or more years. Similarly, Kagarise Sherman (1980) found that only 7% of 522 males captured over multiple years were thought to have skipped one or more years. Other studies of the closely related *A. boreas* reported that < 25% (Olson 1992) and 31% (Bull and Carey 2008) of males skipped one or more years of breeding. Muths et al. (2006, 2010) found some evidence for temporary emigration in both male and female *A. boreas*.

Multi-scale and long term monitoring.—When designing a monitoring program, the information objectives and scale are interrelated. There has been a recent emphasis on monitoring occupancy because it is more feasible for bioregional scale, long-term programs and it is robust to population fluctuations that have been documented in many amphibians at local scales (Corn et al. 2005; MacKenzie et al. 2006; Gould et al. 2012). Yet occupancy is a relatively coarse measure of population dynamics; declines in abundance may precede the distributional changes measured by occupancy (Beiswenger 1986; Collen et al. 2011). Results from this monitoring demonstrate the value of occupancy, abundance, and demography data. The bioregional

occupancy data provide affordable robust broad-scale information and suggest that the Yosemite Toad is still widespread relative to 1990 distributions, the abundance data collected in the intensive meadows suggest that populations may be small, and the demography data provides insights on vital rates. For some species, such as the highly aquatic mountain yellow-legged frogs (*Rana muscosa* and *R. sierrae*), it may be possible to collect both occupancy and relative abundance data bioregionally (Cathy Brown et al., unpubl. data; also Hecnar and M'Closkey 1997; Bonardi et al. 2011). This is not feasible given the Yosemite Toad's ecology, and even for the mountain yellow-legged frogs, obtaining other demographic information (e.g., survival) is not pragmatic rangewide.

Our monitoring results agree with other studies that have found that survey results vary depending on scale. Spatially, Hecnar and M'Closkey (1997) concluded that determination of the status of the Green Frog, *Lithobates (Rana) clamitans*, was dependent on spatial scale and that assessments conducted at smaller scales can lead to incorrect inferences. We also found that occupancy variability depended on scale. Annual variability in occupancy at the site scale of individual lakes, meadows, and stream reaches was higher than at the watershed scale. Given our rotating panel design, single visits at the site scale once every five years may under represent occupancy; however, occupancy was fairly consistent from year to year at the watershed scale. Temporally, longer time series have been shown to be critical for separating short-term fluctuations from longer term trends. Studies have documented large fluctuations in population abundances (Pechmann et al. 1991; Semlitsch et al. 1996; Gibbs et al. 1998; Meyer et al. 1998; Raithel et al. 2011) and site occupancy (Skelly et al. 2003; Trenham et al. 2003) that occur naturally, but do not necessarily reflect declines (see Alford and Richards 1999). We have completed only one monitoring cycle in the extensive component and the time series for our abundance estimates in the intensive meadows is relatively short (four years). Completion of additional monitoring cycles will determine if our initial spatial and temporal occupancy and abundance patterns are consistent over the long term.

Conservation and management.—Management strategies may differ if animals remain in the same sites every year, if different sites are occupied different years (e.g., metapopulation, Levins 1970), or if there is a site that provides most of the recruitment for a cluster of sites (mainland, MacArthur and Wilson 1967; source population, Pulliam 1988). For example, if certain sites are always used for breeding then protection could focus on these. Alternatively, if a variety of sites are used from year to year and by different life stages then a wider protective zone including connectivity among both

consistently occupied and occasionally occupied sites may be more appropriate. Preliminary interpretation of our monitoring results in combination with the knowledge that adults use additional habitats (Karlstrom 1962; Kagarise Sherman 1980; Martin 2008; Liang 2010) suggests that a combination of these approaches is warranted. Identification and additional protection for "mainland" breeding sites is clearly important, but our results suggest that management also consider incorporating broader protection zones that include adult habitats and "island" sites. Further, understanding the annual variation of occupancy can inform decisions on monitoring design. For example, if a species is found in the same places every year, it may be possible to gain efficiencies by making less frequent visits to the same locations. Conversely, if they do not occupy a location every year, it may be necessary to survey more often to have confidence in trend estimates. Our data suggest that at the watershed scale, occupancy is fairly consistent from year to year and is strongly related to snowpack. However, at the site scale, less frequent visits may miss occupancy in some sites.

The Yosemite Toad appears to have declined over a longer time span, yet still persists in the majority of watersheds occupied since 1990. The declines in occupancy from historical locations and the apparent small population sizes in at least two locations merit the development of proactive conservation actions. Research on potential causes and possible mitigation measures is needed. This baseline assessment of status provides data to inform management decisions for the Yosemite Toad and is the foundation for subsequent trend evaluation. By continuing to track trends over time, we will be able to evaluate management success and will provide an early warning system to facilitate proactive conservation planning. Data collected through the program has given us both quantitative and qualitative insights on the status and ecology of this sensitive species which benefit its conservation.

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