

Time-to-detection occupancy methods: performance and utility for improving efficiency of surveys

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Abstract. Occupancy methods propelled the quantitative study of species distributions forward by separating the observation process, or the imperfect detectability of species, from the ecological processes of interest governing species distributions. Occupancy studies come at a cost, however: the collection of additional data to account for nondetections at sites where the species is present. The most common occupancy designs (repeated-measures designs) require repeat visits to sites or the use of multiple observers or detection methods. Time-to-detection methods have been identified as a potentially efficient alternative, requiring only one visit to each site by a single observer. A comparison of time-to-detection methods to repeated-measures designs for visual encounter surveys would allow researchers to evaluate whether time-to-detection methods might be appropriate for their study system and can inform optimal survey design. We collected time-to-detection data during two different repeated-measures design occupancy surveys for four amphibians and compared the performance of time-to-detection methods to the other designs using the location (potential bias) and precision of posterior distributions for occurrence parameters. We further used results of time-to-detection surveys to optimize survey design. Time-to-detection methods performed best for species that are widespread and have high detection probabilities and rates, but performed less well for cryptic species with lower probability of occurrence or whose detection was strongly affected by survey conditions. In all cases, single surveys were most efficient in terms of person-hours expended, but under some conditions the survey duration required to achieve high detection probabilities would be prohibitively long for a single survey. Regardless of occupancy survey design, time-to-detection methods provide important information that can be used to optimize surveys, allowing researchers and resource managers to efficiently achieve monitoring and conservation goals. Collecting time-to-detection data while conducting repeated-measures occupancy surveys requires only small modifications to field methods but could have large benefits in terms of time spent surveying in the long term.

Key words: amphibian; double-observer sampling; occurrence; precision; repeated-measures design; sampling efficiency; survey design.

INTRODUCTION

Occupancy methods revolutionized studies of species occurrence and distributions. They allow researchers to account for the imperfect detectability of animals, plants, and microbes, thereby disentangling the observation process from the ecological process of interest governing the distribution of species (MacKenzie et al. 2002, 2006, Tyre et al. 2003, Bailey et al. 2004). The widespread incorporation of occupancy techniques has resulted in improvements to delimiting the distribution of species and understanding the variables shaping these

distributions. Indeed, failing to account for imperfect detection and covariates of detection probability can lead to improper conclusions about what shapes species' distributions (Tyre et al. 2003, Kéry 2010, Kéry and Schaub 2012).

Occupancy studies, however, come at a cost: the collection of data appropriate to distinguish true absences from non-detections at sites where the species is present. In the most common case, the repeat visits design, a number of sites are surveyed multiple times over a short enough period that the sites are assumed closed to colonization and extirpation, and the pattern of detections and non-detections provides information about the probability of detecting a species, given that it occurs at a site (MacKenzie and Royle 2005, MacKenzie et al. 2006, Kéry and Royle 2016). The repeat visits design

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and its variations, such as removal designs, independent double-observer surveys, or using multiple methods of detection (collectively referred to hereafter as repeated-measures designs), are used in most occupancy studies, and for good reason. These designs are robust and allow great flexibility in modeling the detection process (MacKenzie and Royle 2005), but they require multiple visits to sites, multiple observers, multiple detection methods, or some combination of these. This multiplication of survey effort generally increases the costs associated with estimating and monitoring species occurrence.

Fortunately, a more efficient occupancy design using time-to-detection data requires only a single visit to sites by a single observer (Garrard et al. 2008, 2015, McCarthy et al. 2013, Bornand et al. 2014, Halstead et al. 2018). This gain in efficiency is achieved by using the time between the initiation of a survey and the time at which the first individual of a species is detected to estimate the detection rate, and from that derive the detection probability given survey duration and conditions. Time-to-detection methods have been used successfully for plants (Garrard et al. 2008, 2015, McCarthy et al. 2013, Bornand et al. 2014), amphibians (Halstead et al. 2018), birds (Whittington et al. 2019), and mammals (Medina-Romero et al. 2019). Nonetheless, an empirical test of time-to-detection methods against known occurrence found overestimates of detection probability and underestimates of occupancy when heterogeneity in detection probability was not accounted for (Medina-Romero et al. 2019). This bias is not unique to time-to-detection methods, however, and any accounting for detection probabilities will improve estimates of occurrence relative to naïve estimates that fail to account for imperfect detectability (Guillera-Arroita et al. 2014). Comparisons of time-to-detection methods to repeated-measures designs demonstrated that the former can perform well for plants (Bornand et al. 2014) and birds (Henry et al. 2020), but rare or inconspicuous species present challenges for time-to-detection methods. Few guidelines exist, however, regarding when to use time-to-detection surveys versus repeated-measures occupancy designs to make the best use of limited funding for surveys. Optimizing occupancy surveys is essential for resource managers, who often face the mandate of monitoring species of conservation concern with limited funding (Reich 2020).

The purpose of our study was to empirically compare the performance of single-survey time-to-detection occupancy methods with repeated-measures designs in visual encounter surveys of animals, and use the information generated from time-to-detection methods to develop optimal occupancy surveys. We incorporated time-to-detection into two types of repeated-measures occupancy studies for four amphibians and compared the location and precision of posterior distributions for occurrence parameters for each species. We provide information about the circumstances under which each survey design performed well to help researchers design efficient

occupancy studies. We further demonstrate how one can optimize occupancy surveys by incorporating time-to-detection methods into repeated-measures occupancy designs.

METHODS

Data collection

We collected data using multiple occupancy methods concurrently to assess the efficiency of time-to-detection methods relative to double-observer and repeat visit designs in two different studies (Fig. 1). In 2018, we surveyed for three species of amphibian (Yosemite toad, *Anaxyrus canorus*; Sierran treefrog, *Pseudacris sierra*; and Sierra Nevada yellow-legged frog, *Rana sierrae*) at all lakes, ponds, pools, meadows, and streams (total of 257 sites) within 16 randomly selected long-term monitoring watersheds in Yosemite National Park, USA (hereafter Yosemite NP; Fellers et al. 2015) using the independent double-observer variation of the repeated-measures design. In this study, observers slowly walked through meadows, along streams, and along pond and lake margins visually searching for all amphibians. In addition to recording the counts of each life stage of each species during surveys, technicians recorded the survey time until the first detection of any life stage of each of the three species. To minimize violations of closure for counts but to allow disturbed animals to resume normal behavior, the second observer initiated the survey 15–120 minutes after the first observer.

We also compared time-to-detection techniques to a repeat visits design using surveys for Dixie Valley toads (*Anaxyrus williamsi*) endemic to Churchill County, Nevada, USA. Because the distribution of these toads is so limited (Forrest et al. 2017, Gordon et al. 2017), we did not survey natural wetland units, but instead randomly selected 60 20×20 m plots using a Generalized Random Tessellation Stratified (GRTS) sample (Stevens and Olsen 2004). After marking the center and corners of each plot, observers independently surveyed each plot two to three times over six days (15–20 May 2019; 42 plots were surveyed twice, 18 plots were surveyed three times). Based on a pilot study (Halstead et al. 2019), we instructed observers to survey each plot for a minimum of 15 minutes and set a maximum survey duration of 20 minutes to ensure that each plot was surveyed multiple times. In addition to counts of each life stage of Dixie Valley toads, observers recorded the time elapsed until the first observation of a Dixie Valley toad of any life stage within a plot.

In each study, we collected information on variables thought to affect occurrence, detection, or both. In Yosemite NP, we recorded date and time of the beginning of the survey, weather conditions (cloud cover, wind speed, air and water temperature), site characteristics (mean and maximum water depth, site area, water clarity, percent cover of emergent and floating vegetation,

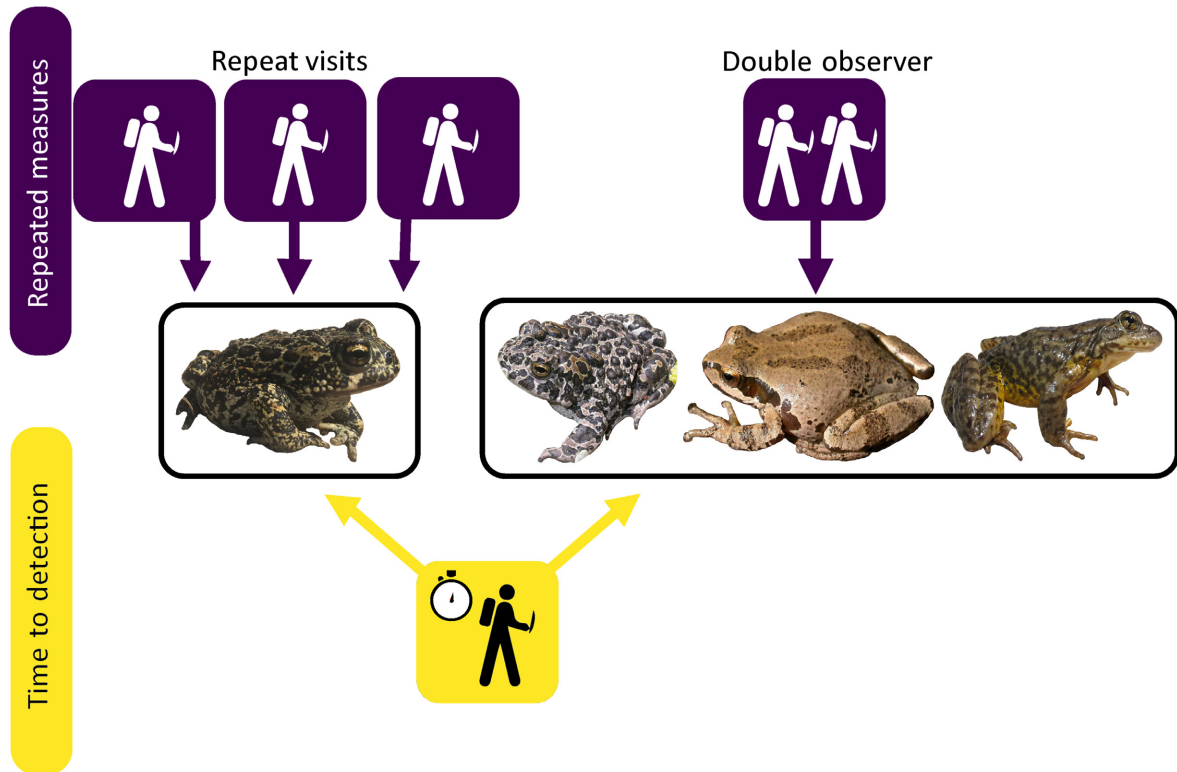


FIG. 1. Diagram illustrating the occupancy survey designs used in this study. We used repeat visits for Dixie Valley toads (*Anaxyrus williamsi*) in Dixie Meadows, Nevada, USA, and independent double-observer surveys for three species (Yosemite toads, *A. canorus*; Sierran treefrogs, *Pseudacris sierra*; and Sierra Nevada yellow-legged frogs, *Rana sierrae*) in Yosemite National Park, California, USA. We also recorded the time to first detection of each species.

permanence of water, presence of flow, detection of fish, substrate type [organic or mineral], and survey duration. For Dixie Valley toads, we recorded the same information, but added proportion of survey plot with surface water, which might influence the occurrence of this species in its shallow desert spring habitat. Data used in this study are available as a USGS data release (Halstead and Kleeman 2020a,b).

Data analysis

To compare time-to-detection methods with other methods for quantifying detection probability, we first selected among competing models of the same sampling method using variable selection techniques (Kuo and Mallick 1998, Hooten and Hobbs 2015). Briefly, we placed indicator variables with Bernoulli(0.5) priors on model coefficients to act as switches that turn effects of predictor variables on (indicator = 1) or off (indicator = 0) at each iteration of the Markov chain Monte Carlo (MCMC) algorithm. In the simplest linear case (i.e., without nonlinear effects or interactions), the posterior probability of inclusion of a predictor variable is the mean of the indicator variable for that predictor in the MCMC output (i.e., the proportion of iterations in

which the variable was turned on). If this posterior probability of inclusion is >0.5 (the prior probability of inclusion specified by the Bernoulli(0.5) prior above), the predictor variable is retained as having greater posterior than prior support, given the model, priors, and data. To avoid sensitivity of model selection to prior distributions on model coefficients (Link and Barker 2010), we used hierarchical shrinkage priors for the coefficients (Kruschke 2015; Appendix S1; Table S1).

For the data from Yosemite NP, we evaluated the same set of predictor variables on detection and occurrence for all species. In particular, we examined the effects of day of year (linear and quadratic effects), time of day (linear and quadratic effects), cloud cover (binary; 0 = clear or partly cloudy, 1 = mostly cloudy or overcast), wind speed (binary; 0, calm or light winds; 1, moderate or heavy winds), air temperature, mean water depth, site area, turbidity (binary; 0, clear; 1, turbid), percent cover of emergent vegetation, and observer (binary) on the probability of detection (p ; double-observer design) and the mean time to detection (μ). Mean time to detection is related to the detection rate, λ , as $\lambda = 1/\mu$, and to detection probability as $p = 1 - e^{-\lambda t}$, where t is the survey duration (Garrard et al. 2008). For probability of occurrence (ψ), we evaluated effects of

mean water depth (linear and quadratic), percent cover of emergent vegetation (linear and quadratic), percent cover of floating vegetation (linear and quadratic), whether the water body was permanent (1) or ephemeral (0), whether fish were detected (0, not detected; 1, detected), whether the substrate was organic (1) or mineral (0), whether the site was lentic (0) or lotic (1), and site area. We standardized all continuous predictor variables to have a mean of zero and standard deviation of one prior to analysis. For all variables for which quadratic effects were evaluated, we required that linear effects were included in the model as well.

Because the sites were artificially defined and the number of sites was smaller for Dixie Valley toads, we evaluated fewer predictor variables for these data. In particular, we evaluated the effects of wind (binary), air temperature, mean water depth, and percent emergent vegetation as fixed effects, and observer as a random effect, for p and μ . For ψ , we evaluated the effects of the proportion of the plot that had surface water, mean water depth, percent emergent vegetation (linear and quadratic), and because the study system had both hot and cold springs, water temperature (linear and quadratic). As with the Yosemite NP data, we standardized all continuous predictors and required that linear effects be included with quadratic effects. For all species, we used the time-to-detection of the first individual regardless of life stage. To better represent how data would typically be collected in a time-to-detection study, we only used the time-to-detection data for the first survey of each site. The full model structure for the repeated-measures occupancy models was

$$\begin{aligned} \text{logit}(\psi_i) &= \beta_0 + \sum_{k=1}^{k=4} (\omega_k \times \beta_k \times x_{i,k}) \\ &\quad + \sum_{k=5}^{k=6} (\omega_{1:2} \times \omega_k \times \beta_k \times x_{i,k}^2) \\ z_i &\sim \text{Bernoulli}(\psi_i) \\ \text{logit}(p_{i,j}) &= \alpha_0 + \sum_{k=1}^{k=4} (v_k \times \alpha_k \times x_{i,j}) + v_5 \times \eta_{\text{obs},i,j}, \text{ and} \\ y_{i,j} &\sim \text{Bernoulli}(z_i \times p_{i,j}) \end{aligned}$$

where ψ is the probability of occurrence, β are coefficients for predictors of occurrence, ω are indicator variables on occurrence coefficients for variable selection, x are predictor variables (x_5 and x_6 are quadratic effects), z is the true occupancy state, p is the probability of detection, α are coefficients for predictors of detection, v are indicator variables on detection coefficients for variable selection, η_{obs} is random variation in detection probability among observers (note that observer was treated as a fixed effect for data from Yosemite NP), and $y_{i,j}$ is the matrix of indicators for detection at each site i in each survey j . Following Garrard et al. (2008), the full

model structure for the time-to-detection occupancy models was

$$\begin{aligned} \text{logit}(\psi_i) &= \beta_0 + \sum_{k=1}^{k=4} (\omega_k \times \beta_k \times x_{i,k}) + \sum_{k=5}^{k=6} (\omega_{1:2} \times \omega_k \times \beta_k \times x_{i,k}^2) \\ \text{log}(u_i) &= \alpha_0 + \sum_{k=1}^{k=4} (v_k \times \alpha_k \times x_{i,k}) + v_5 \times \eta_{\text{obs},i} \\ \lambda_i &= \frac{1}{\mu_i} \\ pp_i &= \psi_i \times \lambda_i \times e^{-\lambda_i \times t_{\text{det},i}} \\ pn_i &= \psi_i \times e^{-\lambda_i \times t_{\text{survey},i}} + (1 - \psi_i) \end{aligned}$$

where ψ , β , ω , x , α , v , and η_{obs} are as defined above, and μ is the time to detection, λ is the detection rate, t_{det} is the time to detection, and t_{survey} is the total survey time. The response variable y_i is a vector of ones used to implement the “ones trick” in Just Another Gibbs Sampler (JAGS) such that if the time to detection is less than the total survey time (i.e., the species was detected), then $y_i \sim \text{Bernoulli}(pp_i)$, and if the species was not detected, then $y_i \sim \text{Bernoulli}(pn_i)$ (Garrard et al. 2008). JAGS code for both models is included in the supporting information (Data S1: JAGS_model_code_for_TTD_and_RM_occupancy_analyses.R).

After selecting the variables important for detection and occurrence of each species under each occupancy study design, we fit a parsimonious model that was a reduced version of the full models considered above. For detection, we included those predictor variables that had a greater marginal posterior probability than prior probability (0.5 for linear effects, 0.25 for quadratic effects because quadratic effects included the linear component, which controls the location of the extremum). Because different variables could be selected for occurrence under the different study designs, for parsimony we selected only those variables with support (greater marginal posterior than prior probability as defined above for detection) in both time-to-detection and repeated-measures occupancy designs. We then plotted posterior distributions under each occurrence model and compared the posterior distributions to evaluate differences in location and precision.

We used the posterior distributions for model parameters to generate detection probability curves (plots with survey duration on the x-axis and detection probability on the y-axis) and examined the optimal survey design for each examined species. We define optimal for our study as the most cost-effective survey design that reaches a specified cumulative detection probability. Using the equation $p = 1 - (1 - p^*)^{(1/n)}$, we estimated the duration of each survey required to reach p (single-survey detection probability) high enough to achieve an arbitrary target cumulative detection probability (p^*) of

0.9 if $n = 1-4$ surveys were conducted. The optimal occupancy survey design was that which minimized cost (person-hours for set up and surveys) while having 95% certainty in achieving the benchmark minimum cumulative detection probability (i.e., the 0.05 quantile of the posterior distribution for $p^* \geq 0.90$). We calculated the total time spent on surveys as the sum of set up time, survey time, and transit time between sites. Set up time for the three species in Yosemite NP included the time needed for a crew of two observers to hike into and out of the 16 watersheds. Set up time for Dixie Valley toads included the time needed to lay out a 20×20 m quadrat, once per site. We assumed a 10-minute transit time between all sites to provide a fair comparison among species and methods. We then compared these results to naïve repeated-measures occupancy designs using multiple surveys of identical duration.

We selected priors for all models to be vague (Appendix S1: Tables S1 and S2) and analyzed all models using Bayesian inference by MCMC methods. To obtain posterior inference, we sampled each model using five independent chains of 20,000 iterations each after an adaptation + burn-in phase of 1,000 + 9,000 iterations by calling JAGS 4.3.0 (Plummer 2017) from R version 3.6.0 (R Core Team 2018) using the package `runjags` (Denwood 2016). We assessed convergence by examining history plots and the partial scale reduction factor (psrf; Gelman and Rubin 1992) and model fit using posterior predictive distributions with a χ^2 discrepancy measure and Bayesian P values (Gelman et al. 1996, Kéry 2010). All psrf values for final models were < 1.01 , and the minimum effective sample size across all parameters of all models was 3,994. We report all posterior distributions as mode (95% highest posterior density interval) unless otherwise indicated.

RESULTS

Comparison of time-to-detection with repeated-measures design

Time-to-detection and double-observer methods performed well for all species examined, with Bayesian P values of 0.238–0.706 for the former and 0.155–0.377 for the latter. Posterior distributions for all parsimonious model parameters related to occurrence broadly overlapped, with similar posterior modes and 95% highest posterior density intervals (Fig. 2). In most cases, posterior distributions were slightly more precise using repeated-measures designs than time-to-detection methods, but differences were small (Fig. 2). Below we compare species-specific results for repeated-measures and time-to-detection designs.

We detected Yosemite toads at 36 sites (14%), with detections by the first observer at 24 sites (9%). Mean time to detection (μ) for Yosemite toads under average survey conditions was predicted to be mode = 142 minutes (95% highest posterior density interval = 66–160

minutes), and the rate at which probability of detection increased with survey duration depended on survey conditions (Appendix S1: Table S3; Fig. 3; Appendix S1: Fig. S1). Single-survey detection probability (p) under the double-observer design for Yosemite toads was 0.11 (0.05–0.20) and was affected by similar variables as time to detection (Appendix S1: Table S3; Appendix S1: Fig. S2). The parsimonious model for probability of occurrence was the null model, although evidence existed for an effect of area and a quadratic effect of water depth using double-observer methods (Appendix S1: Table S4). Estimates of Yosemite toad occupancy were slightly lower for time-to-detection than double-observer methods (time-to-detection $\psi = 0.38$ [0.24–0.57]; double-observer $\psi = 0.43$ [0.29–0.61]; Appendix S1: Fig. S3), and estimates were marginally more precise with double-observer methods (Fig. 2).

We detected Sierran treefrogs at 166 sites (65%), with detections by the first observer at 156 sites (61%). Mean time to detection for Sierran treefrogs under average survey conditions was 1.4 (1.1–1.9) minutes, and the probability of detection rapidly increased with survey duration under most survey conditions (Appendix S1: Table S3; Fig. 4; Appendix S1: Fig. S4). Based on double-observer surveys, p for Sierran treefrogs was 0.96 (0.92–0.98) and was affected by survey conditions (Appendix S1: Table S3; Appendix S1: Fig. S5). The parsimonious model for Sierran treefrog occurrence included effects of fish, substrate, and a quadratic effect of emergent vegetation (Appendix S1: Table S4; Appendix S1: Fig. S6). Effect sizes were generally estimated to be similar in time-to-detection and double-observer models, with double-observer methods being consistently slightly more precise than time-to-detection methods (Fig. 2; Appendix S1: Fig. S6).

We detected Sierra Nevada yellow-legged frogs at 102 sites (40%), with detections by the first observer at 97 sites (38%). Mean time to detection for Sierra Nevada yellow-legged frogs under average survey conditions was 3.2 (2.3–4.6) minutes and detection probabilities increased rapidly and plateaued as survey duration increased, except when emergent vegetation cover was high (Appendix S1: Table S3; Fig. 5; Appendix S1: Fig. S7). Under average survey conditions, double-observer p for Sierra Nevada yellow-legged frogs was 0.95 (0.86–0.99), but p varied with conditions such as cloud cover, site area, and water depth (Appendix S1: Table S3; Appendix S1: Fig. S8). The parsimonious model for Sierra Nevada yellow-legged frogs included effects of fish and water flow on occurrence (Appendix S1: Table S4; Appendix S1: Fig. S9). Effect sizes were generally similar for both survey methods, with coefficients of double-observer methods being consistently slightly more precise than time-to-detection methods, but the intercept being slightly more precise with time-to-detection methods (Fig. 2; Appendix S1: Fig. S9).

We detected Dixie Valley toads at 17 sites (28%), with detections in the first survey at 14 (23%) sites. For Dixie

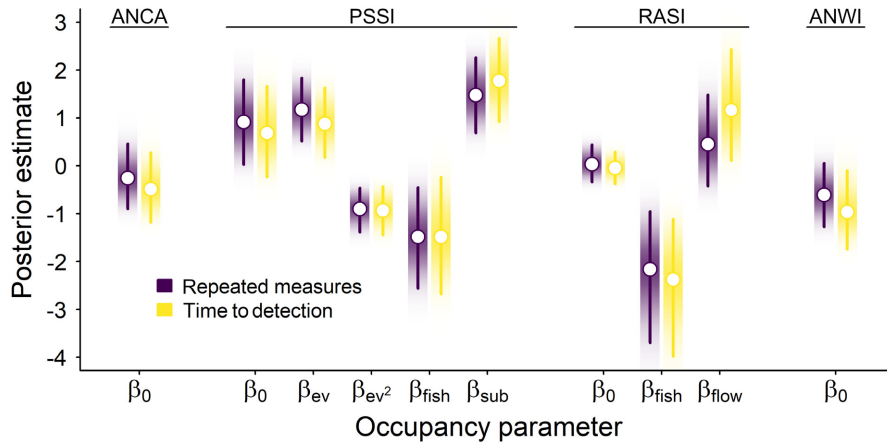


FIG. 2. Comparison of posterior distributions of occupancy parameters estimated using repeated-measures (indigo) and time-to-detection (gold) occupancy surveys. All parameters are presented on the logit scale. Parameter posterior distributions are clustered by species, indicated by the code at the top of the figure (ANCA, Yosemite toad, *Anaxyrus canorus*; PSSI, Sierran treefrog, *Pseudacris sierra*; RASI, Sierra Nevada yellow-legged frog, *Rana sierrae*; ANWI, Dixie Valley toad, *A. williamsi*). Points represent posterior modes, vertical lines represent 95% highest posterior density intervals, and the intensity of shading represents posterior probability densities. Abbreviations: ev, percent cover of emergent vegetation; sub, organic substrate. Note that differences between parameters located at greater absolute values on the logit scale represent relatively smaller differences on the probability scale than the same differences for parameters closer to zero. See Appendix S1: Figs. S3, S6, S9, and S13 for comparisons of posterior distributions plotted on the probability scale.

Valley toads, no predictors of time to detection were selected, but air temperature was found to affect the repeat visits probability of detection (Appendix S1: Table S5). The mean time to detection for Dixie Valley toads was 5.4 (2.7–17.6) minutes (Appendix S1: Fig. S10), and the predicted probability of detection plateaued for survey durations ≥ 15 minutes (Appendix S1: Fig. S11). Dixie Valley toad p under average conditions using the repeat visits design was 0.58 (0.38–0.75) and was positively related to air temperature (Appendix S1: Fig. S12). The parsimonious model of Dixie Valley toad occurrence did not include any of the measured variables (Appendix S1: Table S6). Although the precision of ψ was similar for repeat visits and time-to-detection methods, the time-to-detection model estimated ψ to be slightly lower than the repeat visits design estimate (Fig. 2; Appendix S1: Fig. S13). With the time-to-detection model, ψ was estimated to be 0.27 (0.15–0.47), whereas with the repeat visits model, ψ was estimated to be 0.35 (0.22–0.51; Appendix S1: Fig. S13).

Survey optimization

To achieve $p^* \geq 0.9$ requires one survey with $p \geq 0.90$, two surveys with $p \geq 0.68$, three surveys with $p \geq 0.54$, or four surveys with $p \geq 0.44$. For all species, a single longer-duration survey was most efficient in terms of total person-hours expended, but survey durations required to achieve $p^* \geq 0.9$ with 95% certainty varied greatly among species (Table 1). The additional cost to conduct two surveys rather than one, assuming survey duration was set by the minimum required to achieve $p^* \geq 0.9$ with 95% confidence, was 1.5% greater for

Yosemite toads, 11% greater for Sierran treefrogs and Sierra Nevada yellow-legged frogs, and 10% greater for Dixie Valley toads. If survey duration was fixed at 15 minutes across scenarios (rather than optimized to achieve a desired p^*), then the increased cost to conduct two surveys rather than one after accounting for set up costs would be 23% for double-observer surveys at Yosemite NP and 34% for repeat visits surveys for Dixie Valley toads. The detection probabilities achieved by these short, fixed-duration surveys demonstrate the inefficiency of this approach by either failing to achieve desired cumulative detection probabilities or expending unnecessary survey effort (Table 2). For Yosemite toads, even four 15-minute surveys fail to achieve $p^* \geq 0.9$ with 95% confidence. In contrast, for Sierran treefrogs and Sierra Nevada yellow-legged frogs, even one 15-minute survey could be more effort than is needed to achieve the desired level of cumulative detection probability under average conditions (Table 2).

Heterogeneity in time-to-detection induced by survey conditions also can be used to optimize occupancy surveys (Figs. 3–5). For example, to achieve $p \geq 0.9$ with 95% certainty in a single survey at an average site for Sierran treefrogs on 15 July, when larvae are large and active, would require a survey duration of 5 minutes, whereas on 1 September, when metamorphosis has occurred and juveniles have dispersed from many sites, 53 minutes would be required to achieve the same p (Fig. 4). For Sierra Nevada yellow-legged frogs at a site with no emergent vegetation, a single survey of 3 minutes duration achieves $p \geq 0.9$ with 95% certainty, whereas at a site with 50% emergent vegetation, achieving the same detection probability would require 38 minutes of survey time

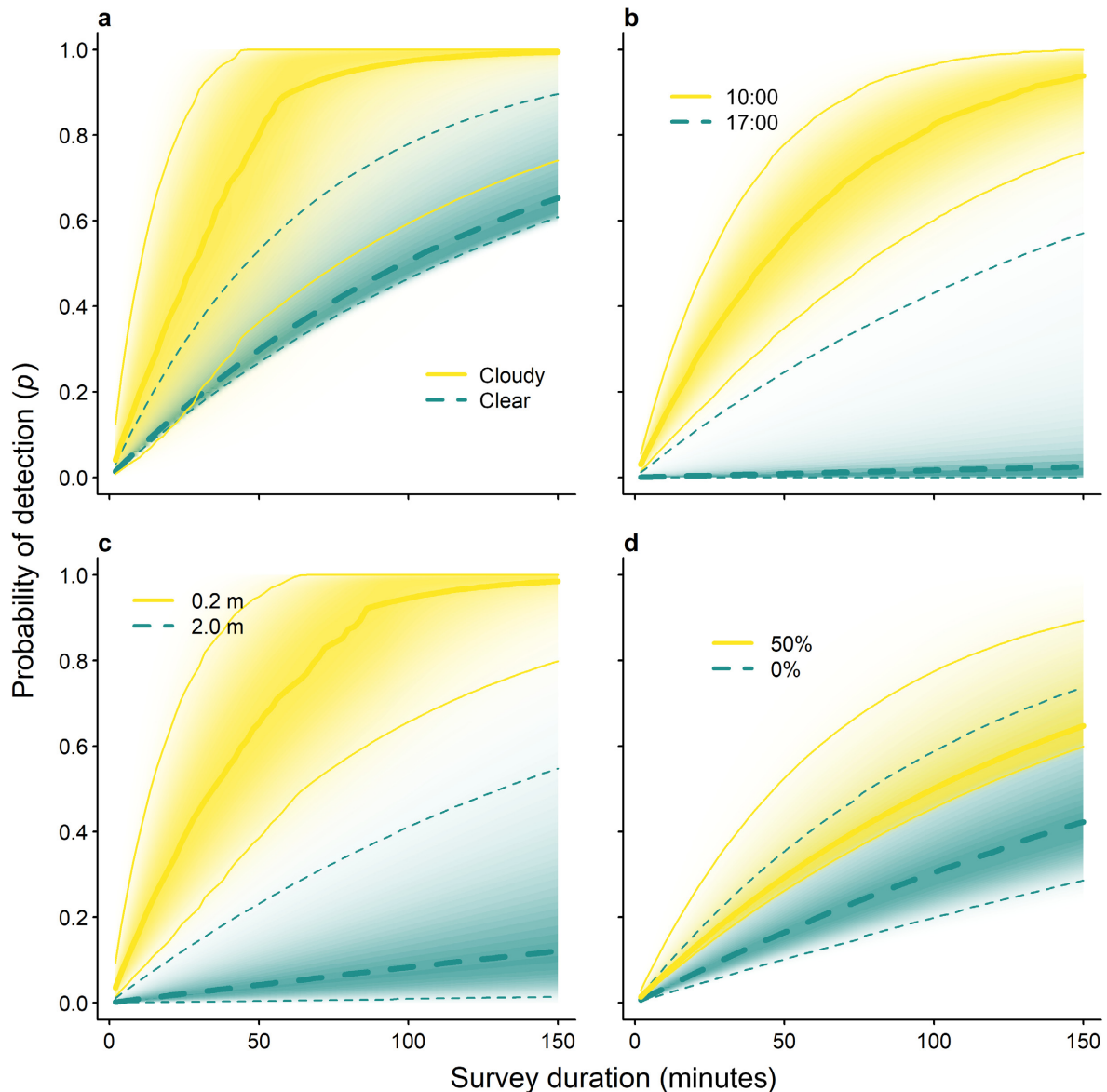


Fig. 3. Effects of survey duration on detection probability (p) under different scenarios of (a) cloud cover, (b) time of day, (c) water depth, and (d) emergent vegetation cover for Yosemite toads (*Anaxyrus canorus*) in Yosemite National Park, USA, 2018. Heavy lines represent posterior modes, light lines represent 95% highest posterior density interval limits, and the intensity of shading represents the posterior probability density. For each panel, other variables were held constant at their mean value.

(Fig. 5). Cloud cover, time of day, and water depth all have large effects on the survey duration needed to achieve $p \geq 0.9$ for Yosemite toads (Fig. 3).

DISCUSSION

Time-to-detection occupancy methods can efficiently estimate the probability of occurrence of animals while accounting for imperfect detection, but they have important limitations. For easy-to-detect species present at a high proportion of sites, time-to-detection methods are

as effective as repeated-measures designs but require half the effort to implement in the field once sites are reached. For rare or cryptic species, the survey time required to achieve high p using a single survey with time-to-detection methods may be too long to be practical. Heterogeneity in detection rates further limits the utility of time-to-detection methods when the conditions under which surveys are conducted cannot be controlled. Collecting time-to-detection data, however, provides information relevant to designing efficient occupancy surveys regardless of the study design

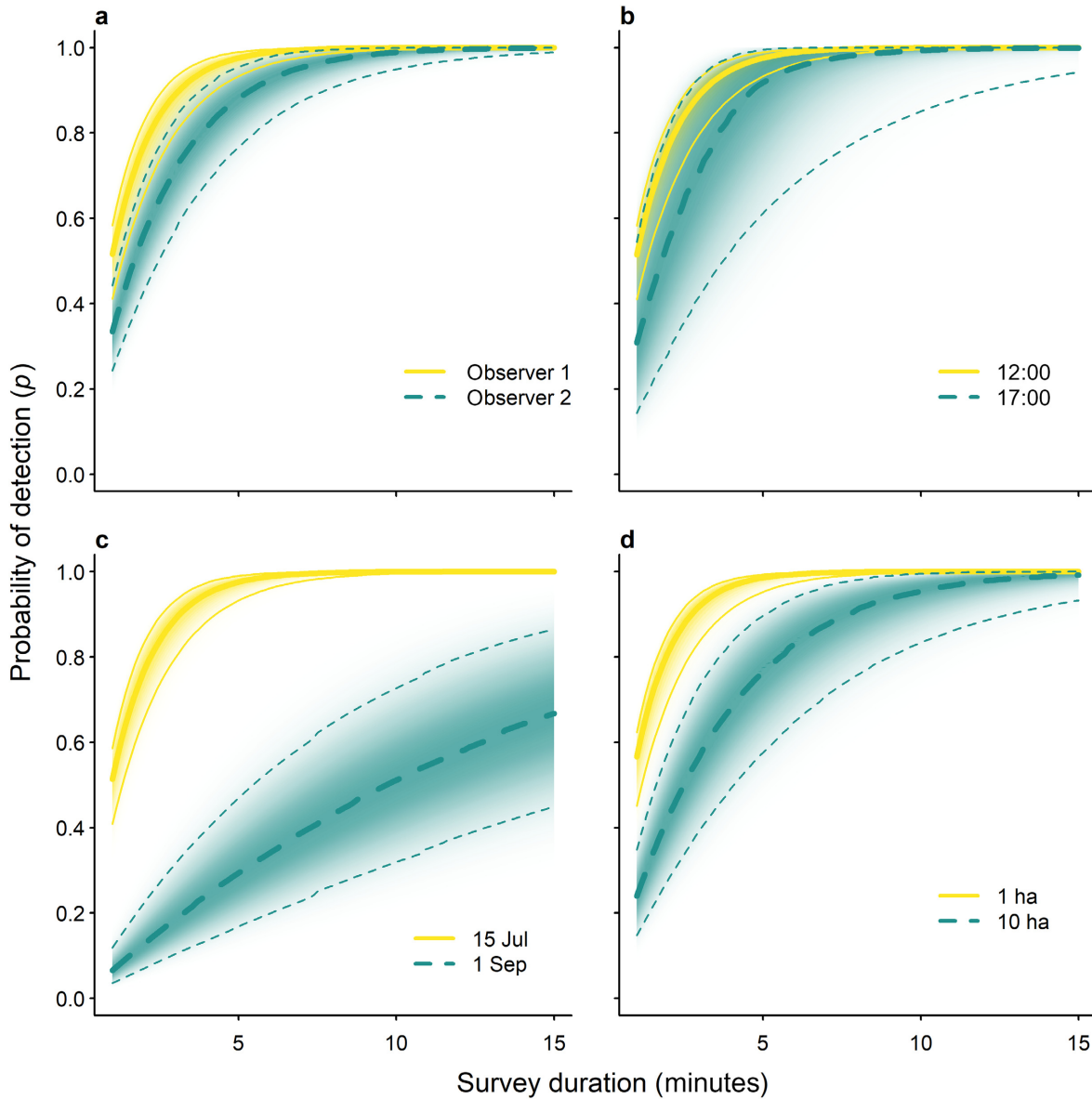


FIG. 4. Effects of survey duration on detection probability (p) under different scenarios of (a) observer, (b) time of day, (c) date, and (d) site area for Sierran treefrogs (*Pseudacris sierra*) in Yosemite National Park, USA, 2018. Heavy lines represent posterior modes, light lines represent 95% highest posterior density interval limits, and the intensity of shading represents the posterior probability density. For each panel, other variables were held constant at their mean value.

ultimately chosen. Perhaps most importantly, time-to-detection occupancy methods and repeated-measures designs produce similar posterior inference about species occurrence.

For nearly all parameters, repeated-measures designs resulted in more precise posterior distributions than time-to-detection methods. The gain in precision in most cases, however, was minimal. For Sierran treefrogs and Sierra Nevada yellow-legged frogs, the large number of sites with detections by the first observer (156 [61%] and

97 [38%], respectively) resulted in ample information to estimate the time-to-detection and variables affecting detection rate, and inference from time-to-detection and double-observer methods was very similar. Both toad species, however, were detected by the first observer or in the first survey at fewer sites (24 [9%] for Yosemite toads and 14 [23%] for Dixie Valley toads), resulting in less information with which to estimate the time to initial detection. Nonetheless, the precision of the posterior distributions for occupancy was similar for time-to-

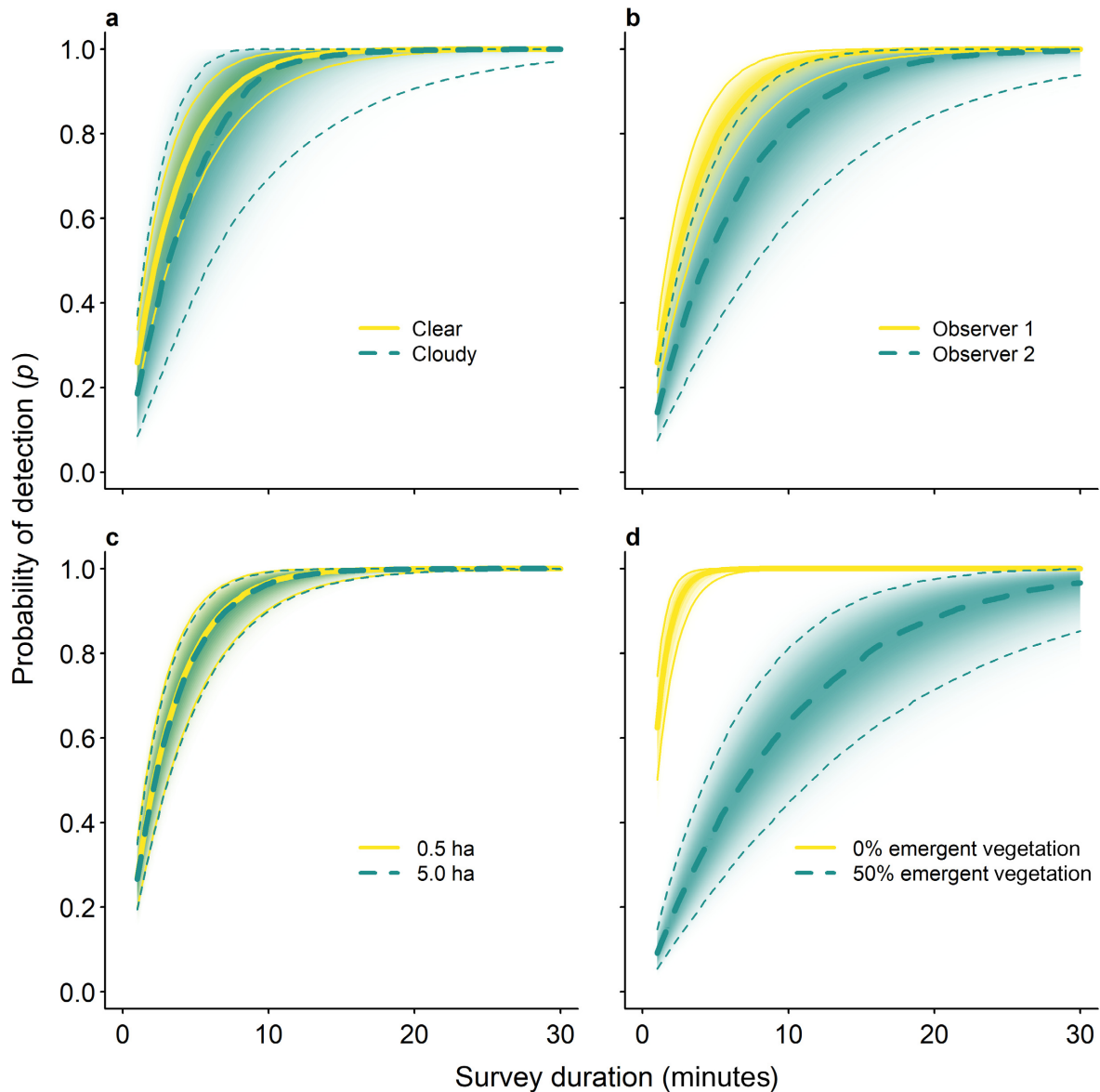


Fig. 5. Effects of survey duration on detection probability (p) under different scenarios of (a) cloud cover, (b) observer, (c) area, and (d) emergent vegetation cover for Sierra Nevada yellow-legged frogs (*Rana sierrae*) in Yosemite National Park, USA, 2018. Heavy lines represent posterior modes, light lines represent 95% highest posterior density interval limits, and the intensity of shading represents the posterior probability density. For each panel, other variables were held constant at their mean value.

detection and repeated-measures surveys (Fig. 2). Even where posterior distributions differed between occupancy designs, their precision often differed by less than their location.

Perhaps more problematic than a slight decrease in precision is potential bias in estimates of occupancy. For both toad species, time-to-detection methods resulted in slightly lower occupancy estimates (Fig. 2; Appendix S1: Figs. S3, S13) similar to the downward bias reported in a study with known occurrence (Medina-Romero et al. 2019). Two different mechanisms could lead to lower

occupancy estimates. First, in repeated-measures designs two or more opportunities exist to detect the species of interest, whereas time-to-detection methods offer only one such opportunity. Detections of the species at subsequent surveys increases the minimum proportion of occupied sites, resulting in an increase in the lower limit of the finite-sample occurrence rate (Royle and Dorazio 2008, Link and Barker 2010), and therefore, a general increase in the location for the posterior distribution for probability of occurrence. We expect that this phenomenon will be especially pronounced for species with

TABLE 1. Number of person-hours required to set up and conduct surveys to achieve cumulative detection probability $p^* \geq 0.90$ with 95% certainty under average or reference survey conditions with different numbers of surveys of varying duration.

Species	Set up time (h)	One survey		Two surveys		Three surveys		Four surveys	
		Survey duration (minutes)	Total time (h)	Survey duration (minutes)	Total time (h)	Survey duration (minutes)	Total time (h)	Survey duration (minutes)	Total time (h)
Yosemite toad	352	361	1,942	179	1,972	122	2,049	91	2,083
Sierran treefrog	352	5	417	3	464	2	507	2	558
Sierra Nevada yellow-legged frog	352	11	442	6	489	4	532	3	575
Dixie Valley toad	48	40	98	20	108	14	120	10	128

Notes: Survey duration is for each individual survey. Total time includes set up time, survey time, and 10 minutes for transit between sites. The number of sites for Yosemite toads (*Anaxyrus canorus*), Sierran treefrogs (*Pseudacris sierra*), and Sierra Nevada yellow-legged frogs (*Rana sierrae*) was 257, with set up time being the time to hike into and out of 16 watersheds using a crew of 2 (for safety); the number of sites for Dixie Valley toads (*A. williamsi*) was 60 with a single set up period.

TABLE 2. Cumulative detection probability achieved under naive repeated-measures designs with surveys of constant 15-minute duration for Yosemite toads (*Anaxyrus canorus*), Sierran treefrogs (*Pseudacris sierra*), Sierra Nevada yellow-legged frogs (*Rana sierrae*), and Dixie Valley toads (*A. williamsi*).

Species	Number of 15-minute surveys			
	1	2	3	4
Yosemite toad	0.10 (0.09–0.20)	0.19 (0.17–0.36)	0.27 (0.25–0.49)	0.35 (0.31–0.60)
Sierran treefrog	>0.99 (>0.99–>0.99)	>0.99 (>0.99–>0.99)	>0.99 (>0.99–>0.99)	>0.99 (>0.99–>0.99)
Sierra Nevada yellow-legged frog	0.99 (0.97–>0.99)	>0.99 (>0.99–>0.99)	>0.99 (>0.99–>0.99)	>0.99 (>0.99–>0.99)
Dixie Valley toad	0.94 (0.58–>0.99)	>0.99 (0.82–>0.99)	>0.99 (0.93–>0.99)	>0.99 (0.97–>0.99)

Notes: Cumulative detection probabilities are based on average survey conditions. Values in the table are presented as mode (95% highest posterior density interval) to represent most likely values.

low detection probabilities (e.g., the cryptic species of Specht et al. [2017] or very inconspicuous species of Henry et al. [2020]), where subsequent surveys are likely to discover the species in sites where it was previously undetected. In these instances, it is likely that one could reduce this potential bias by increasing survey duration or by limiting surveys so that they are conducted only under ideal survey conditions, thereby increasing the detection rate and minimizing heterogeneity in time-to-detection. Whether these changes to survey design are feasible will vary with the study system.

The second mechanism that could result in lower occupancy estimates in time-to-detection methods is violation of the closure assumption (MacKenzie et al. 2006, Rota et al. 2009, Bornand et al. 2014, Kéry and Royle 2016). Indeed, if the closure assumption is violated, then the difference in occupancy estimates is likely an upward bias when using repeated-measures designs (Rota et al. 2009), rather than a downward bias in time-to-detection methods. This mechanism is unlikely in the case of double-observer surveys, where we restricted surveys to be conducted within 2 h of each other, but could be problematic in repeat visits designs if the time between surveys is long relative to site colonization and extirpation dynamics. Even with all surveys being conducted within

6 d, if the 20 × 20 m survey plots were small relative to Dixie Valley toad movements, occupancy estimates could be biased high (and detection probabilities biased low) using the repeat visits design. Thus, one potential advantage of time-to-detection methods is that sites should remain closed to colonization and extirpation during the single survey for all but the most mobile animals and smallest sites.

Time-to-detection methods offer a further advantage regarding survey design. By plotting detection probability against survey duration, it is possible to calculate the optimal survey duration to achieve a desired minimum detection probability. In our example, we further considered the time associated with set up and transit between sites. In all cases, a single survey of longer duration was the most efficient in terms of person-hours, but some caveats to this pattern exist. For example, the gain in efficiency (time required to achieve $p^* \geq 0.9$ with 95% certainty) by conducting a single survey was highest for Sierran treefrogs and Sierra Nevada yellow-legged frogs, nearly as high for Dixie Valley toads, and much lower for Yosemite toads. In many cases, however, the survey duration required to achieve high p was prohibitively long. This was true for nearly all conditions for Yosemite toads. For Dixie Valley toads, we expect that surveying a

20 × 20 m plot for 40 minutes would tax the attention span of many observers; in this case, conducting two independent surveys of 20 minutes duration might be a better choice. Thus, human nature, as well as efficiency, should be taken into consideration when planning occupancy surveys.

Accounting for heterogeneity in detection rates further highlights advantages associated with using time-to-detection methods to optimize survey design. By using within-survey information on detection rates, survey duration can be optimized for survey conditions. Under many circumstances, this optimization can be done prior to a field visit, for example, by accounting for known site conditions or the date when surveys will be conducted. In other cases, optimization could entail limiting the conditions under which surveys can be conducted, for example, by limiting surveys to a certain time of day or weather conditions. Optimization becomes more difficult for multi-species occupancy surveys (Henry et al. 2020) where detectability curves for the same variable often differ among species.

A further consideration in the choice between time-to-detection and repeated-measures surveys is availability for detection (Bornand et al. 2014). Seasonal or daily activity patterns or movement can affect availability for detection, as can the sensitivity of the target organism to environmental conditions at the time of the survey. If the target organism is unavailable for detection under certain conditions, then surveys will fail to detect the species regardless of survey duration. A single visit under suboptimal conditions might also increase the time to initial detection to the extent that the target organism is undetected at a high proportion of sites where it occurs. In this regard, repeated-measures designs will be more effective because independent surveys will likely encompass a broader range of environmental conditions, both increasing the power to estimate the effects of survey conditions on detection and increasing the likelihood that at least one survey at a site will occur when the target organism is both available and likely to be detected. For example, detection probability was highly dependent on survey conditions for Yosemite toads, and a single long-duration survey on a clear sunny day might not be as informative as shorter surveys conducted on multiple days, if conditions are cloudy on one of those days (Fig. 3). As information is gained about the detection process, survey protocols can be optimized to minimize time-to-detection and maximize detection probability regardless of occupancy study design (Bornand et al. 2014, Reich 2020), and multiple time-to-detection surveys also could be conducted (Henry et al. 2020).

Whether time-to-detection methods represent a gain in efficiency also is affected by the relative cost of repeated surveys. For example, if the initial survey is substantially more expensive than subsequent surveys (e.g., if setting up survey quadrats takes a substantial amount of time), then conducting time-to-detection surveys (or other survey modifications, such as removal or

conditional sampling; MacKenzie and Royle 2005, Specht et al. 2017) will result in fewer gains in efficiency than if all surveys incur the same implementation cost. In our case, even after accounting for implementation costs, a single survey was always technically the most cost-effective, although in some cases (e.g., Yosemite toads) the duration required for a single survey would be prohibitive.

Several factors therefore affect the decision between using time-to-detection and repeated-measures studies of occurrence. Time-to-detection methods perform best when (1) the target organism is widespread, occurring at a large number of sites to allow estimation of parameters affecting time to detection (Bornand et al. 2014, Henry et al. 2020); (2) detection probabilities are relatively high, so the first survey is reasonably likely to result in detection of the target organism if it is present (Henry et al. 2020); (3) detection of the target organism varies relatively little with environmental conditions at the time of the survey, environmental conditions change little across surveys, or surveys can be planned for optimal survey conditions; and (4) set up costs are minimal, so that subsequent surveys are not appreciably cheaper than the initial survey. Some of these factors are under the control of the researcher, and one might be able to increase the number of sites or survey duration to meet conditions 1 and 2, whereas set up costs and conducting surveys only under ideal conditions might be more difficult to control. Perhaps more important than choosing between repeated-measures and time-to-detection designs, however, is that incorporating time-to-detection into repeated-measures surveys is straightforward and can allow researchers to optimize surveys for their study system.

In summary, time-to-detection occupancy methods can perform as well as repeated-measures designs under realistic field conditions and offer the advantage of providing important information relevant to optimizing surveys. Careful pilot studies incorporating time-to-detection methods into repeated-measures surveys allow the evaluation of both methods and can help researchers optimize occupancy protocols for their study system. In many cases, time-to-detection methods offer improved efficiency relative to repeated-measures occupancy study designs, allowing researchers to sample more sites with the same limited budget. The efficiency of time-to-detection methods for many organisms will reduce financial barriers to accounting for imperfect detection in occupancy studies and improve inference about species distributions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2267/full>

DATA AVAILABILITY

Site and survey data used in this study are available on ScienceBase: amphibian surveys (Halstead and Kleeman 2020a) <https://doi.org/10.5066/P9DM40GP>; Dixie Valley toads (Halstead and Kleeman 2020b) <https://doi.org/10.5066/P9BT38WU>.