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Research Article

Bayesian Adaptive Survey Protocols for Resource Management

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ABSTRACT Transparency in resource management decisions requires a proper accounting of uncertainty at multiple stages of the decision-making process. As information becomes available, periodic review and updating of resource management protocols reduces uncertainty and improves management decisions. One of the most basic steps to mitigating anthropogenic effects on populations is determining if a population of a species occurs in an area that will be affected by human activity. Species are rarely detected with certainty, however, and falsely declaring a species absent can cause improper conservation decisions or even extirpation of populations. We propose a method to design survey protocols for imperfectly detected species that accounts for multiple sources of uncertainty in the detection process, is capable of quantitatively incorporating expert opinion into the decision-making process, allows periodic updates to the protocol, and permits resource managers to weigh the severity of consequences if the species is falsely declared absent. We developed our method using the giant gartersnake (*Thamnophis gigas*), a threatened species precinctive to the Central Valley of California, as a case study. Survey date was negatively related to the probability of detecting the giant gartersnake, and water temperature was positively related to the probability of detecting the giant gartersnake at a sampled location. Reporting sampling effort, timing and duration of surveys, and water temperatures would allow resource managers to evaluate the probability that the giant gartersnake occurs at sampled sites where it is not detected. This information would also allow periodic updates and quantitative evaluation of changes to the giant gartersnake survey protocol. Because it naturally allows multiple sources of information and is predicated upon the idea of updating information, Bayesian analysis is well-suited to solving the problem of developing efficient sampling protocols for species of conservation concern. © 2011 The Wildlife Society.

KEY WORDS Bayesian inference, California, decision analysis, giant gartersnake, occurrence, survey design, *Thamnophis gigas*, uncertainty.

Accounting for imperfect detection in demographic studies is of paramount importance for estimating population parameters (Williams et al. 2002, Mazerolle et al. 2007). Errors arising from imperfect detection are particularly egregious for rare species, which are often difficult to detect (MacKenzie et al. 2004). For rare, difficult to detect species, wrongly declaring the species absent from a site can result in inappropriate conservation action, or worse, extirpation of populations. Therefore, survey protocols for rare species, in particular, need to pay careful attention to the problem of imperfect detectability and quantify uncertainty associated with declaring the species absent from a site.

Occupancy modeling is a particularly useful approach for quantifying uncertainty in the occurrence of a species (MacKenzie et al. 2002). Occupancy models involve repeated surveys, usually (though not necessarily) consisting of multiple visits to several sites (MacKenzie et al. 2006). These multiple site visits allow estimation of the probability of detecting the species, and heterogeneity in the detection process can often be attributed to site, temporal, and temporally varying site characteristics (Royle 2006). Once the probability of detecting the species in a given survey has been determined, the minimum number of surveys required to infer its absence, given a specified level of confidence, is straightforward (Kéry 2002, Wintle et al. 2005). Although general guidelines exist for designing occupancy studies (MacKenzie and Royle 2005), few standardized protocols for surveys of rare species are based upon explicit quantification of detectability (but see Wintle et al. 2005, Driscoll 2010).

Bayesian analysis of occupancy models offers several potential advantages over frequentist analysis of such models. Small sample sizes are typical in resource management settings, and Bayesian inference is exact, regardless of sample size, whereas frequentist inference often requires asymptotic

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approximations, meaning that estimates of uncertainty are valid for large samples only (Royle and Dorazio 2008, Kéry 2010, Link and Barker 2010). Bayesian inference is also more intuitive for many people because it expresses confidence in the distribution of a parameter rather than confidence that an interval contains the true value of the parameter, as in frequentist inference. Another advantage of Bayesian inference for the resource manager is that accounting for propagation of error is straightforward and does not require approximations like the delta method (Williams et al. 2002, Kéry 2010). Prediction is similarly straightforward and can be directly implemented into the analysis or derived from posterior distributions of parameters. The use of prior information, when available, is another advantage of the Bayesian approach to statistical analysis; the fear that such prior information taints results can be assuaged by performing a prior sensitivity analysis (Link and Barker 2010).

The giant gartersnake (*Thamnophis gigas*) is a large (to 1.6 m total length), semi-aquatic snake precinctive to the Central Valley of California (Fitch 1940, Hansen and Brode 1980). Because of its limited distribution and the loss of nearly 90% of its original wetland habitat to agricultural and other development (Frayer et al. 1989), the giant gartersnake is listed as threatened by both the United States Fish and Wildlife Service (USFWS 1993) and the California Department of Fish and Game (1971). The giant gartersnake is both wary and cryptic, and it readily drops from emergent vegetation into water upon approach (Hansen 1980). In addition to its ability to evade surveyors, the giant gartersnake also exhibits extensive periods with little or no movement, often in burrows or deep cracks in the soil (G. D. Wylie, U.S. Geological Survey, unpublished data). These characteristics make the giant gartersnake difficult to survey. Because of difficulty surveying the giant gartersnake and conservation concern for this species, it is imperative that surveys conducted for the species quantify the degree of confidence in declaring the species absent from sites where potential negative effects of anthropogenic activities have been identified.

Our objective was to develop a repeatable, quantitative survey protocol for the giant gartersnake that accounts for uncertainty in model selection and parameter estimation. In particular, we were interested in developing a method that allows identification of the variables affecting detection probability and using the resulting model to develop repeatable survey methods. We illustrate the utility of our method with an analysis of the detectability of the giant gartersnake and propose a standardized survey method based upon our results.

STUDY AREA

We surveyed for the giant gartersnake in >100 locations in the Central Valley of California, USA, from 2003 through 2009. Sampling effort was predominantly within the Sacramento Valley (northern portion of the Central Valley), but some sites were located in the San Joaquin Valley (southern portion of the Central Valley) and the Sacramento-San Joaquin Delta region as well. The geographic location of survey sites was based upon locations of funded projects.

METHODS

We sampled the giant gartersnake using transects of 10–398 ($\bar{x} = 59$) floating aquatic funnel traps (Casazza et al. 2000). Within a site, individual transects were located in areas of standing or slow-moving water and, where possible, emergent aquatic vegetation. These characteristics are important attributes of giant gartersnake habitat for foraging and cover from predators (G. D. Wylie, unpublished data). We placed traps approximately 10 m apart in water deep enough to float the traps ($\geq$10 cm) and placed them so funnel openings were along a bank or the edge of emergent vegetation wherever possible. We deployed traps and monitored them daily during the active season of the giant gartersnake (Apr to Oct) each year for 12–142 consecutive days. We measured several transect characteristics, including habitat type (canal vs. wetland), the number of individual giant gartersnakes captured each day, the number of traps deployed, and daily surface water temperature at the time of sampling. We handled snakes in accordance with University of California–Davis Animal Care and Use Protocol (protocol 9699) and as stipulated by USFWS (Recovery Permit TE-020548-5).

We determined the effect of multiple variables on detection probability (p) of the giant gartersnake in trap transects using a Bayesian analysis of logistic regression models (Royle and Dorazio 2008, Kéry 2010). We split our data into 2 parts, using data collected from 2003 through 2006 ($n = 67$ transects) for the initial development of the survey protocol and data from 2007 through 2009 ($n = 22$ transects) to demonstrate the process of periodically updating the protocol. In practice, one would use all available data for development of the survey protocol. We developed a model for p that contained several covariates that could either be determined a priori by the surveyor or that could easily be measured before or during sampling. We treated each transect as a site in our analysis. Site covariates we included in our model included habitat type (wetland or canal, which specified the presence of a steep bank to act as a drift fence); an index of snake abundance, calculated as the maximum number of individuals captured in one sampling event (day) divided by the number of traps in the transect; and the number of traps deployed. In addition to these site covariates, we also examined the influence of water temperature and time of year (days since 1 Apr) on p. We included a quadratic effect of time of year to determine if an optimal time of year for sampling existed. We centered and standardized each continuous variable and specified a random site effect for p to account for differences in detection probability not attributable to measured variables. We selected important variables and determined posterior model probabilities by associating an indicator variable with each coefficient and determining the frequency of each unique combination of indicator variables in the Markov chain Monte Carlo (MCMC) output (Kuo and Mallick 1998, Royle and Dorazio 2008). We used posterior model probabilities to calculate model-averaged

parameter estimates. Our full model was therefore:

$$\log\left(\frac{p_{ij}}{1-p_{ij}}\right) = a_0 + w_1 a_1 \text{habitat}_i + w_2 a_2 \text{popindex}_i + w_3 a_3 \text{trapno}_i + w_4 a_4 \text{watertemp}_{ij} + w_5 a_5 \text{date}_{ij} + w_5 w_6 a_6 \text{date}_{ij}^2 + \varepsilon_i,$$

where p_{ij} is the detection probability at site i on occasion j, w_k is the indicator variable for predictor k, a_k is the coefficient for predictor k, and $\varepsilon_i \sim N(0, \sigma)$ is the random site effect.

We fit the model using 2 sets of priors applied to the 2003–2006 data and updated the results of the uninformative priors with the 2007–2009 data (Table 1). We selected the first set of priors for the 2003–2006 data to be uninformative and the second set represented informative priors based upon expert opinion derived from data collected prior to 2003. The informative prior distribution of the mean intercept expressed past experience that, on average for most sites at which the giant gartersnake occurs, about 10% of daily surveys result in detection (G. D. Wylie, unpublished data; Table 1). The informative gamma prior on the site standard deviation had mean = variance = 1. We based informative priors for number of traps, water temperature, and date upon correlation of these variables with the number of snakes captured in previous studies. We reflected the prior distribution at zero to limit effects to either positive or negative (G. D. Wylie, unpublished data; Table 1). For variables with no data upon which to base informative priors (i.e., habitat type, population index, and quadratic effect of date), expert opinion was expressed as a half-normal (standard N(0, 1)) distribution to represent expectations that effects were positive or negative (Table 1). The third set of priors was the posteriors from the uninformative analysis of 2003–2006 data; we used these priors to update the model with data collected 2007–2009 (Table 1). Regardless of the priors used or data analyzed, we conducted the analysis using MCMC methods as implemented in WinBUGS 1.4.3 (Spiegelhalter et al. 2003) with 5 chains of 200,000 iterations each, thinned by a factor of 100 after 20,000 burn-in iterations. We selected starting values for each parameter in each chain to be reasonable, but dispersed enough to assess convergence (Table 1). We examined history plots and the Gelman–Rubin statistic (Gelman et al. 2004) as calculated by package coda (Plummer et al. 2008) for each parameter for evidence of lack of convergence. We determined the adequacy of our model with a posterior predictive model check using a Bayesian P-value (Kéry 2010, Link and Barker 2010).

We used the posterior predictive distribution from the updated model to determine the probability that hypothetical surveyed sites were occupied, given that no detections occurred. We specified the data for the hypothetical sites to indicate the effect of survey conditions on inferring that a species is absent, given that it is not detected. Our standard survey consisted of 50 traps deployed in a canal on 1 June in 25 ± 1.5°C ($\bar{x}$ ± SD) water for either 28 consecutive days or 56 consecutive days. From these standard conditions, we systematically varied the starting date of the surveys (early = 1 Apr, late = 1 Aug) and water temperature (hot = 30 ± 1.5°C, cold = 20 ± 1.5°C). We drew daily water temperatures from a normal distribution with specified mean and standard deviation. We calculated the expected daily capture probability for each hypothetical site from the current draw from the posterior distribution at each iteration, and we drew an occupancy indicator for each hypothetical site from a Bernoulli distribution. To specify prior ignorance on the occupancy status of the hypothetical sites, we specified a Be(1, 1) prior on the probability of occupancy (ψ), and we drew each site's occupancy indicator from a Bern(ψ) distribution. The posterior mean of the occupancy indicator specifies the posterior probability that the site is occupied, given the survey conditions and no detections. This procedure is readily adapted to actual sites, and informative priors can be used if, for example, surveys in previous years indicated presence of the species or if the site contains high-

Table 1. Prior probabilities and initial values for each parameter of each alternative analysis of the Bayesian logistic regression model we used to develop a survey protocol for the giant gartersnake in the Central Valley of California, 2003–2009.

	Prior probabilities			Initial values	
Parameter[a]	Uninformative	Informative	Update	Uninformative and update	Informative
σ_{site}	U(0, 100)	Gamma(1, 1)	Gamma(76.8, 69.8)	(0.1, 1, 2, 3, 5)	(0.1, 1, 2, 3, 5)
a_0	N(0, 0.0001)	N(−2, 0.25)	N(−1.784, 0.338)	(−5, −2, 0, 2, 5)	(−3, −2.5, −2, −1.5, −1)
a_1	N(0, 0.0001)	−|N(0, 1)|	N(0.0002, 0.029)	(−5, −2, 0, 2, 5)	(−4, −3, −2, −1, 0)
a_2	N(0, 0.0001)	|N(0, 1)|	N(0.069, 0.385)	(−5, −2, 0, 2, 5)	(0, 1, 2, 3, 4)
a_3	N(0, 0.0001)	|N(0.5, 0.2)|	N(0.003, 0.030)	(−5, −2, 0, 2, 5)	(0, 0.5, 1, 1.5, 2)
a_4	N(0, 0.0001)	|N(0.5, 0.25)|	N(0.058, 0.096)	(−5, −2, 0, 2, 5)	(0, 0.5, 1, 1.5, 2)
a_5	N(0, 0.0001)	−|N(−0.5, 0.2)|	N(−0.101, 0.133)	(−5, −2, 0, 2, 5)	(−2, −1.5, −1, −0.5, 0)
a_6	N(0, 0.0001)	−|N(0, 1)|	N(0.000, 0.004)	(−5, −2, 0, 2, 5)	(−4, −3, −2, −1, 0)
w_1	Bern(0.5)	Bern(0.5)	Bern(0.004)	(1, 1, 1, 1, 1)	(1, 1, 1, 1, 1)
w_2	Bern(0.5)	Bern(0.5)	Bern(0.043)	(1, 1, 1, 1, 1)	(1, 1, 1, 1, 1)
w_3	Bern(0.5)	Bern(0.5)	Bern(0.009)	(1, 1, 1, 1, 1)	(1, 1, 1, 1, 1)
w_4	Bern(0.5)	Bern(0.5)	Bern(0.291)	(1, 1, 1, 1, 1)	(1, 1, 1, 1, 1)
w_5	Bern(0.5)	Bern(0.5)	Bern(0.391)	(1, 1, 1, 1, 1)	(1, 1, 1, 1, 1)
w_6	Bern(0.5)	Bern(0.5)	Bern(0.001)	(1, 1, 1, 1, 1)	(1, 1, 1, 1, 1)

[a] σ_{site} = SD of random site effect, a_0 = intercept, a_1 = effect of habitat (canal vs. wetland), a_2 = effect of population index, a_3 = effect of number of traps, a_4 = effect of temperature, a_5 = effect of days since 1 Apr, a_6 = effect of (days since 1 Apr)^2, w_k = indicator variable for selection of model containing variable k.

quality habitat near existing populations. We further calculated the cumulative probability of detecting the giant gartersnake at each hypothetical site, assuming that the giant gartersnake is present. Cumulative probability of detection is the probability that the species will be detected after n surveys, given that it is present at the site, and is a useful metric for planning the number of surveys under specified conditions (Kéry 2002). We calculated cumulative probability of detection as $1-\prod_{i=1}^{n}(1-p_{ij})$, where p_{ij} is the specified quantile of detection probability on survey i at site j, and n is the number of surveys (Kéry 2002).

We conducted all analyses by calling WinBUGS 1.4.3 (Spiegelhalter et al. 2003) from R (R Version 2.11.0, http://www.R-project.org, accessed 25 Jun 2010) using the package R2WinBUGS (Sturtz et al. 2005; Supporting Information Appendix A, available online at www.onlinelibrary.wiley.com). We used the R packages coda (Plummer et al. 2008) to calculate the Gelman–Rubin statistic and data summaries of each parameter and emdbook (Bolker 2007) to format the MCMC output for calculation of derived parameters in R (Supporting Information Appendix A, available online at www.onlinelibrary.wiley.com).

RESULTS

We detected the giant gartersnake at 89 individual transects from 2003 to 2009 (2003–2006 = 67 transects; 2007–2009 = 22 transects). The diagnostic history plots appeared well mixed and the Gelman–Rubin statistic was <1.05 for each monitored parameter when we analyzed the model using uninformative priors. The posterior predictive check for the uninformative analysis also did not indicate model inadequacy (Bayesian P-value = 0.451). With uninformative priors, 5 detection probability models had posterior probabilities >0.01 (Table 2). The best-supported model was the null model of constant detection probability with a random site effect (posterior probability = 0.446). Other supported models included effects of date (0.224), date and water temperature (0.145), and water temperature (0.131; Table 2). Although posterior probability distributions of all model-averaged coefficients contained zero, probability of detecting the giant gartersnake decreased later in the year and increased with increasing water temperature (Fig. 1). Mean daily detection probability was 0.14 (Fig. 1).

Diagnostic history plots appeared well mixed and the Gelman–Rubin statistic was <1.03 for each monitored parameter when we analyzed the model using informative priors. The posterior predictive check for the informative analysis also did not indicate model inadequacy (Bayesian P-value = 0.338). Analysis of the model using priors informed by expert opinion resulted in more highly parameterized models having increased support (Table 2). In particular, the best-supported model with informative priors was that with effects of date, number of traps, and water temperature (0.359; Table 2); these variables also had the strongest prior probabilities. Seven additional models had posterior probabilities >0.01. The best-supported of these models included date and water temperature (0.208); date, number of traps, population index, and water temperature (0.154); date, population index, and water temperature (0.069); and date, habitat, and water temperature (0.054; Table 2). Informative priors decreased the posterior probability of no effect for most parameters and shifted the posterior distribution of most parameters toward the prior mean relative to posteriors based upon analysis of the model with uninformative priors (Fig. 2). Alternatively, we can interpret the posteriors for coefficients of all variables as decreased belief in the magnitude of the effects of each variable on detection probability of the giant gartersnake (Fig. 2).

Table 2. Posterior probabilities of models for the probability of detecting the giant gartersnake in the Central Valley of California from 2003 to 2009.

Parameter[a]						Posterior probability[b]		
Date	Date^2	Habitat	No. traps	Pop. index	Temp	Uninformative	Informative	Update
1	0	0	0	0	1	0.145	0.208	0.894
1	0	0	0	0	0	0.224	0.002	0.038
1	0	0	0	1	1	0.007	0.069	0.035
0	0	0	0	0	1	0.131	0.001	0.014
1	0	0	1	0	1	0.001	0.359	0.010
1	0	1	0	0	1	0.000	0.054	0.003
1	0	0	0	1	0	0.010	0.001	0.002
1	0	0	1	1	1	0.000	0.154	0.001
0	0	0	0	0	0	0.446	0.000	0.000
0	0	0	0	1	0	0.019	0.000	0.000
1	0	1	1	0	1	0.000	0.077	0.000
1	0	1	1	1	1	0.000	0.030	0.000
1	0	1	0	1	1	0.000	0.016	0.000

[a] A "1" indicates that the parameter was included in the model, and a "0" indicates that the parameter was not included in the model. Habitat = habitat type (canal vs. wetland), no. traps = number of traps, pop. index = population size index, and temp = water temp.

[b] Uninformative = posterior probability from analysis of the 2003–2006 data using uninformative priors, expert = posterior probability from analysis of the 2003–2006 data using priors informed by expert opinion, and update = posterior probability from analysis of the 2007–2009 data using posteriors from the uninformative 2003–2006 model as priors. We listed models in order of decreasing posterior probability based upon the updated model, then the model with uninformative priors, and finally the model with informative priors. We included only those models with a posterior probability ≥0.01 for any set of priors or data in the table.

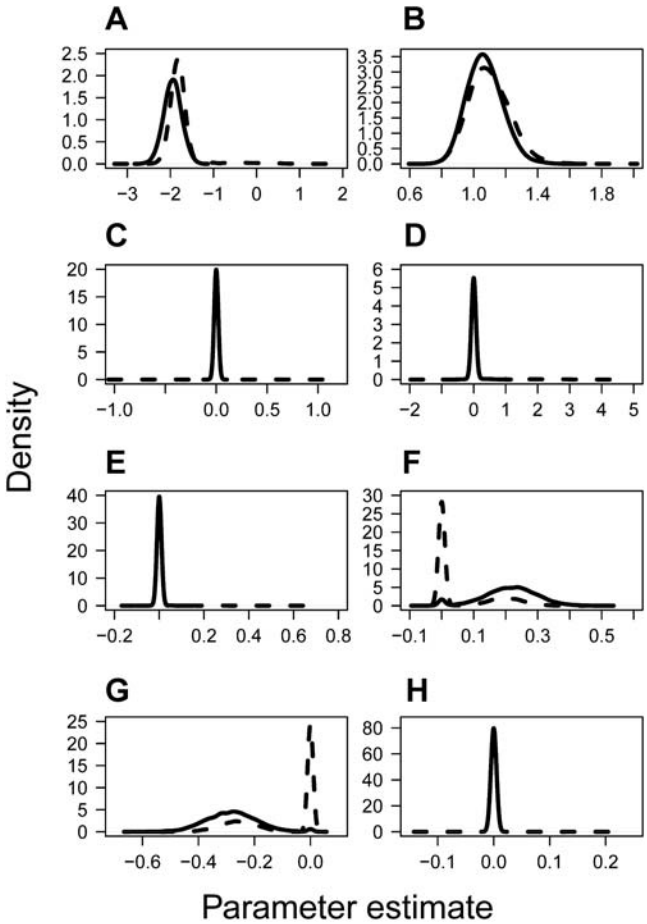

Figure 1. Posterior probability distributions for Bayesian logistic regression model parameters of detection probability for the giant gartersnake in the Central Valley of California, 2003–2009, based upon uninformative prior distributions. A: Mean intercept, (B) standard deviation of intercept, (C) habitat type, (D) population size index, (E) number of traps, (F) water temperature, (G) date, and (H) date^2. Dashed lines indicate initial modeling posterior probability distributions (which we used as prior probability distributions for updating the protocol), and solid lines indicate the updated posterior probability distributions. Bimodal posterior distributions are the result of mixtures representing an increased mass at zero when the indicator for that variable was zero. Note that scales on the axes differ for each plot.

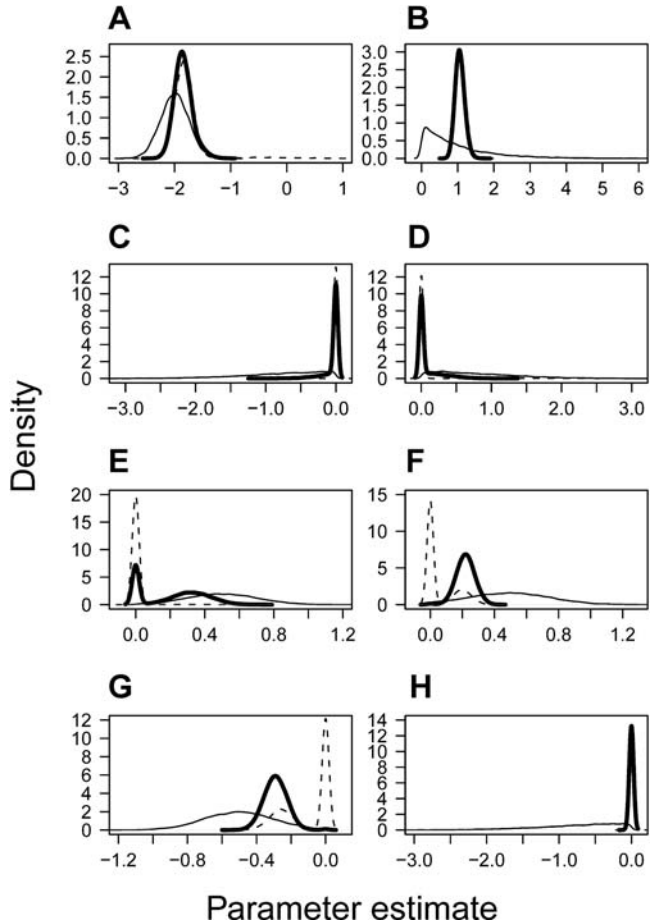

Figure 2. Posterior probability distributions for Bayesian logistic regression model parameters of detection probability for the giant gartersnake in the Central Valley of California, 2003–2009, based upon informative priors representing expert opinion. A: Mean intercept, (B) standard deviation of intercept, (C) habitat type, (D) population size index, (E) number of traps, (F) water temperature, (G) date, and (H) date^2. Heavy solid lines indicate posterior probability distributions, light solid lines indicate prior distributions, and light dashed lines indicate posterior probability distributions from the model fit to the same data using uninformative priors. Note that scales on the axes differ for each plot.

Diagnostic history plots appeared well mixed and the Gelman–Rubin statistic was <1.08 for each monitored parameter of interest when we updated the model with data from 2007 to 2009 using priors informed by uninformed analysis of the 2003 to 2006 data. The posterior predictive check for the informative analysis also did not indicate model inadequacy (Bayesian P-value = 0.566). Updating the model resulted in much greater posterior probability for the model with effects of date and water temperature (0.894; Table 2). Three additional models had posterior probabilities >0.01, but none of these had a posterior probability >0.05. Updated model-averaged posterior distributions were similar to those from the original analysis, except that the negative effect of date and positive effect of water temperature both increased in magnitude (Fig. 1). The model-averaged posterior distribution for the effect of date had a median of −0.279 (95% credible interval = −0.451 to −0.082). These values correspond to daily probability of detecting the giant gartersnake in a transect on 21 August of 0.097 (95% CI = 0.064–0.146), relative to 0.124 (0.087–0.175) on 13 July (the latter date is the mean survey date; the former is 1 SD after mean survey date). The 95% credible interval of this difference is 0.008–0.046. The model-averaged posterior distribution for the effect of water temperature had a median of 0.211 (95% CI = 0.000–0.364), which corresponds with a 0.125 (0.087–0.175) daily probability of detecting the giant gartersnake in 24.5°C water but 0.150 (0.101–0.214) in 27.5°C water. The 95% credible interval of this difference is 0.000–0.049.

The conditions under which we conducted surveys affected the posterior predictive probability that the site was occupied, given that no detections occurred (Table 3). In particular, non-detection surveys consisting of longer sampling periods, earlier in the year, and in warmer water resulted in a lower probability that the site was actually occupied, but the giant gartersnake was missed (Table 3). Similarly, the

Table 3. Probability of occupancy for hypothetical sites surveyed for the giant gartersnake, given no detections under specified conditions, based upon surveys conducted in the Central Valley of California from 2003 to 2009.

Condition[a]	4 weeks of daily surveys ($n = 28$)	8 weeks of daily surveys ($n = 56$)
Early	0.009	0.002
Late	0.019	0.009
Hot	0.006	0.004
Cold	0.012	0.007

[a] Except where indicated, conditions were a small population (index = 0.01 individuals/trap), 50 traps, 25 ± 1.5°C water, and surveys beginning on 1 Jun. Early = surveys beginning 1 Apr, late = surveys beginning 1 Aug, hot = 30 ± 1.5°C water, and cold = 20 ± 1.5°C water. We drew daily water temp from a normal distribution with specified $\bar{x}$ and SD.

cumulative probability of detecting the giant gartersnake was greater earlier in the year and in warmer water (Fig. 3).

DISCUSSION

Our method has several benefits over maximum likelihood-based inference typically used for logistic regression and occupancy modeling. Perhaps the greatest benefit is the ability of Bayesian methods to incorporate prior information into analysis. Expert opinion is often used to develop survey methods for organisms of conservation concern. The Bayesian method we outlined allows the use of expert opinion in a quantitative analysis; one need only specify the prior distribution to represent existing knowledge or opinion. This prior belief in the effects of survey conditions on detection is easily updated with data using MCMC techniques in a Bayesian analysis to obtain posterior inference. Although Bayesian inference is exact for all sample sizes, the more data, the less influence the prior distribution has on the posterior distribution (Gelman et al. 2004, Royle and Dorazio 2008, Link and Barker 2010). In our study, using informative priors based upon expert opinion resulted in additional variables having important consequences for detection probability. In many cases, the retention of variables thought important for explaining the detection process might be a desirable property because it prevents the premature dismissal of these variables when insufficient data exist to provide strong evidence for an effect. On the other hand, if an analysis that disregards prior knowledge is desired, an objective Bayesian analysis can be conducted using diffuse, uninformative priors. The latter analysis will provide posterior inference similar to that obtained with frequentist methods using maximum likelihood estimation (Kéry 2010). In either case, posterior distributions of parameter estimates from these models can be used as priors for an update of the models with new data. Ideally, survey protocols would be re-evaluated periodically as surveys are conducted and additional data accumulated in an adaptive monitoring framework (Wilhere 2002, McCarthy and Possingham 2007).

An additional benefit of Bayesian analysis is the use of the posterior predictive distribution for easily calculating derived parameters. Once the posterior distribution of a parameter is calculated, the posterior distribution of any function of that parameter is readily obtained by simply calculating the desired function using samples from the parameter's posterior distribution (Link and Barker 2010). Frequentist analysis would require use of the delta method to approximate uncertainty associated with derived parameters

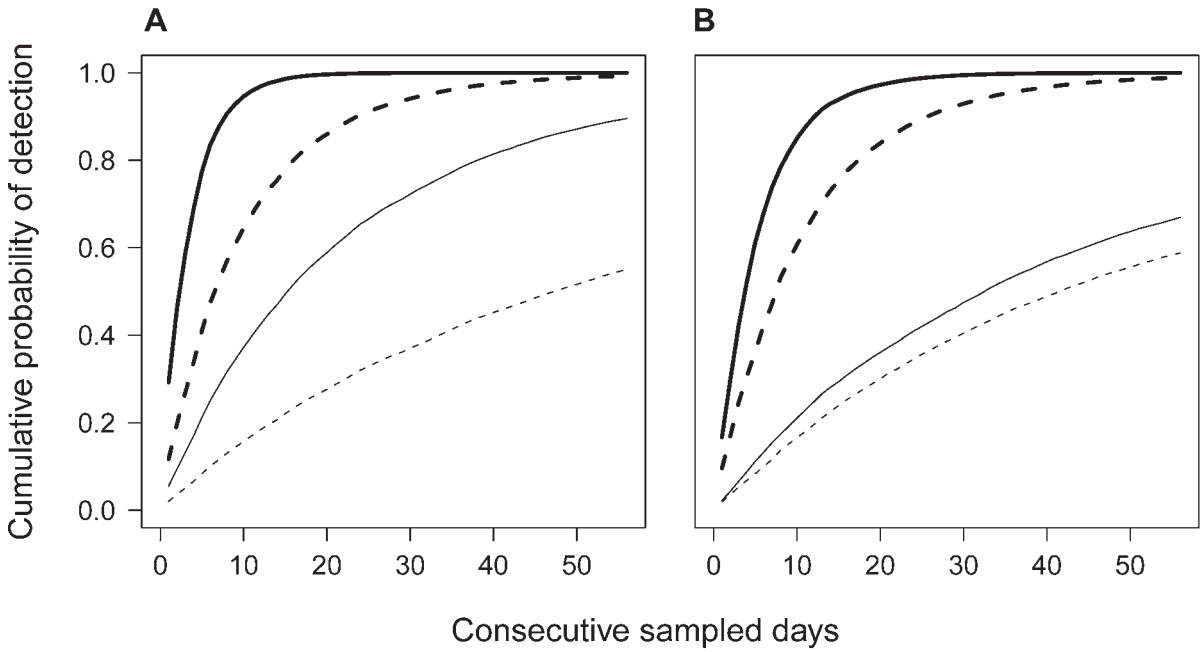

Figure 3. Cumulative detection probabilities for the giant gartersnake in the Central Valley of California, 2003–2009, given occurrence under different scenarios. Except where indicated, conditions were a small population (index = 0.01 individuals/trap), 50 traps, 25 ± 1.5°C water, and surveys beginning on 1 June. In each plot, the heavy line represents the median cumulative detection probability and the light line represents the 0.05 quantile of cumulative detection probability. A: Solid line = surveys beginning 1 April, dashed line = surveys beginning 1 August; and (B) solid line = 30 ± 1.5°C water, dashed line = 20 ± 1.5°C water. We drew daily water temperatures from a normal distribution with specified mean and standard deviation.

(Williams et al. 2002). A related construct is the analysis of hypothetical replicates, which are easily calculated using the Bayesian posterior predictive distribution (see Supporting Information Appendix A, available online at www.onlinelibrary.wiley.com). In our study, using derived parameters and hypothetical replicates allowed prediction of the probability that a hypothetical site that was not in the sample was occupied, given survey conditions, without making the asymptotic assumptions required to do so with a frequentist analysis (Link and Barker 2010).

Our method also explicitly accounts for several sources of uncertainty in developing the survey protocol. We dealt with model selection uncertainty using Bayesian multimodel inference (Royle and Dorazio 2008, Link and Barker 2010), which is analogous to model averaging using information criteria, such as Akaike's Information Criterion (AIC). Model selection uncertainty is an important, but often overlooked, source of uncertainty in resource management that should be honestly accounted for in management decisions (Wintle et al. 2003, Ellison 2004). We also accounted for uncertainty in parameter estimation by using the entire posterior predictive distribution of parameter estimates for out of sample inference and prediction, which is particularly important when the model contains unexplained heterogeneity in the form of random effects, because unobserved site characteristics can affect the observed response. One potential source of uncertainty that we did not address was that sampled sites at which no detections occur might have actually been occupied, but the giant gartersnake was undetected. We conditioned our analyses on sites known to be occupied to focus inference on the detection process; nonetheless, such additional heterogeneity can often be accounted for in an occupancy model.

Accounting for these various sources of uncertainty might initially appear to make management decisions daunting, but it adds full transparency to the decision-making process and allows resource managers latitude in making management decisions. For example, managers can specify a degree of certainty that a site is not occupied at which a proposed action would be allowed, based upon the severity of the consequences for the species in question, and determine if the posterior predictive distribution of the probability of occurrence exceeds that value, given survey conditions. A liberal assessment for minor impacts might allow a proposed action if the posterior probability of occurrence is less than, for example, 0.1; if the consequences of the proposed action are severe, managers might require a posterior probability of occurrence to be <0.01 (or some other small probability). As an alternative strategy, managers could specify a minimum number of surveys necessary to declare a species effectively absent from a site, given no individuals are detected, based upon the posterior predictive distribution of the cumulative probability of detection under specified conditions (Fig. 3). If a proposed action will not have large negative impacts to the species, the median (e.g., see bold lines in Fig. 3) of this distribution could be used to calculate the number of surveys required to declare the species effectively absent. However, if a proposed action is likely to have dire consequences for a population of an extremely rare species, then managers can use a low quantile of the posterior distribution of detection probability, and therefore require greater survey effort, to declare the species effectively absent from the site (e.g., fine lines in Fig. 3). Of course, management decisions could also account for the value of unoccupied sites for potential colonization, but decision-making in this context is outside the scope of our analytical approach. In many cases, however, management decisions can be made based upon the cost of falsely declaring a species absent, with a transparent accounting of both uncertainty and the decision-making process (Wade 2000). This decision-making process can be formalized in a Bayesian decision analysis, whereby uncertainty in process inputs and outcomes are incorporated into the choice of alternative courses of action (Ellison 1996, Harwood 2000, Wade 2000, Gelman et al. 2004). Wade (2000) provides an approachable example of Bayesian decision analysis for research managers.

MANAGEMENT IMPLICATIONS

Survey conditions influenced the probability of falsely declaring the giant gartersnake absent from a site. Both planning surveys and interpreting survey results must account for effects of survey conditions on detecting the giant gartersnake. We propose several recommendations for a standardized survey protocol for the giant gartersnake. We recommend sampling as early in the active season (after 1 Apr) as possible to increase detection probability. Detection probability also increased with increasing water temperature, thus surveys conducted in cooler water (e.g., irrigation ditches supplied with well water) or during cold weather should include more sampling days. We further recommend that no surveys be commenced after 1 October because of low detection probabilities (late date and likely cold weather) and impending hibernation. Despite the small effect of other variables, we recommend they be recorded (along with any additional information the surveyor thinks is relevant to detectability), because additional data might demonstrate these, and potentially other, variables to be important. This was indeed the case with our analysis, where the null model of no covariate effects had the greatest posterior probability in the preliminary analysis, but no posterior support when we updated the model with additional data. The positive relationship of trap number with detection probability, when a non-zero relationship existed, therefore supports employing as many traps as practical to increase probability of detection. The posterior distributions generated by our analysis can be used to plan future giant gartersnake surveys to maximize detection probabilities and to determine the probability of occurrence of the giant gartersnake at locations with existing non-detection surveys. We recommend that resource management agencies mandate the collection and reporting of detection histories, data on sampling effort and survey conditions, and any modifications to standard protocols in permits for surveys for the giant gartersnake and other species of conservation concern. These data will then be available to periodically update and refine survey protocols (McCarthy and Masters 2005) or calculate the probability

that the species of interest occurred at a location in which it was not detected.

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