

Integrating growth and capture–mark–recapture models reveals size-dependent survival in an elusive species

JONATHAN P. ROSE , † GLENN D. WYLIE , MICHAEL L. CASAZZA , AND BRIAN J. HALSTEAD 

Western Ecological Research Center, Dixon Field Station, U.S. Geological Survey, 800 Business Park Drive, Suite D,
Dixon, California 95620 USA

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Abstract. Survival is a key vital rate for projecting the viability of wild populations. Estimating survival is difficult for many rare or elusive species because recapture rates of marked individuals are low, and the ultimate fate of individuals is unknown. Low recapture rates for many species have made it difficult to accurately estimate survival, and to evaluate the importance of individual and environmental covariates for survival. Individual covariates such as size are particularly difficult to include in capture–mark–recapture models for elusive species because the state of the individual is unknown during periods when it is not captured. Here, we integrate a von Bertalanffy growth model with a multi-state robust-design Cormack–Jolly–Seber model to test for a relationship between body size and survival in the elusive, threatened giant gartersnake, *Thamnophis gigas*. We take a Bayesian approach to model the size of an individual during periods when it was not captured and measured, which fully propagates uncertainty in this unobserved covariate. We found strong support for a positive relationship between snake size and annual survival, with survival increasing with size up to a peak for adult snakes, after which survival either declines slightly or plateaus for the largest individuals. Few captures of very small and very large individuals led to high uncertainty in the survival rates of these sizes. Survival of giant gartersnakes was also positively related to the amount of precipitation and the cover of emergent and floating vegetation at a site. To our knowledge, our study is the first to estimate a size–survival relationship in a snake while fully accounting for uncertainty in the size of unobserved individuals. Our results have implications for the management of this threatened species and illustrate the utility of integrating hierarchical Bayesian models to the study of survival in elusive species.

Key words: Bayesian imputation; conservation; giant gartersnake; hierarchical model; integrated model; missing data.

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† **E-mail:** jprose@usgs.gov

INTRODUCTION

Estimating survival is difficult for rare or elusive species that are infrequently observed or captured (hereafter, “elusive species”). Low capture probabilities lead to high uncertainty in estimates of survival (Pike et al. 2008, Papadatou et al. 2012). One solution to obtain survival estimates when capture probabilities are low is to assume constant survival rates (Pollock et al.

1990). Survival often varies over time and among populations, however (Brown and Weatherhead 1999, Gaillard and Yoccoz 2003, Miller et al. 2011), and it is important to quantify this variation to understand natural population dynamics (Rees and Ellner 2009). Obtaining precise yearly or population-specific survival estimates is even more challenging for elusive species, because increasing the number of parameters to be estimated from sparse data leads to greater

uncertainty for each parameter (Pollock et al. 1990); this can inhibit researchers' ability to estimate annual variation in survival (Hyslop et al. 2012).

Hierarchical capture–mark–recapture (CMR) models that share information about the capture and survival process among populations and years can improve precision of parameter estimates while simultaneously obtaining site- and year-specific estimates (Kéry and Schaub 2012, Papadatou et al. 2012). For example, if a species is sampled using the same methods year after year at several sites, we might expect the capture process to be similar among sites and over time. Rather than treating data from each site and year as independent, a hierarchical model can adaptively pool information on capture probabilities from each site and each year and use these pooled data to improve estimates at each site, in each year (Rivot and Prévost 2002, Halstead et al. 2012). Beyond measuring spatial and temporal variation in survival, quantifying how survival is influenced by environmental factors such as habitat type, climate, and food availability may be key for predicting future population responses to anthropogenic change (Anderson 1988, Altwegg et al. 2005, Todd and Rothermel 2006). Hierarchical models can better quantify how much of the observed variation in survival is attributable to environmental covariates vs. unmeasured heterogeneity among sites and years (Gelman and Hill 2007).

In addition to modeling spatial and temporal variability in survival, ecologists often want to identify factors that explain variation in survival among individuals in the same population. Individual characteristics such as size, age, sex, and body condition can all influence the probability of survival (Stanford and King 2004, Altwegg et al. 2005, Blums et al. 2005). Including age and sex as discrete covariates of survival and capture probability is straightforward, provided an individual's state can be determined during its initial capture. If an individual is captured and classified once, its sex is (usually) fixed and its age increases in a predictable, deterministic fashion. Measures of body size may be more closely related to survival than age, however (Sauer and Slade 1987, Wallace et al. 2013), and some species are difficult to reliably age (Halliday and Verrell 1988). Therefore, a continuous measure of body

size such as mass or length may be a better way to characterize an individual's state for analyses of many demographic processes.

Modeling the relationship between survival and continuous, time-varying individual covariates such as mass, length, or body condition is difficult, because the state of the individual is unknown when it is not captured and measured. This problem is exacerbated for species with low capture probability, because the vast majority of individuals may be captured only once or twice, so most individual covariate data are missing. One solution is deterministic imputation, where values are predicted for the missing covariate data, and these predicted values are treated as observed data in a CMR model (Hansen et al. 2015). This method ignores uncertainty in the missing values and may underestimate the uncertainty in parameter estimates (Bonner et al. 2010). Recently, methods have been developed to include time-varying individual covariates such as body size in CMR models using Bayesian imputation. In Bayesian imputation, a model is used to predict the missing covariate values, and these predicted values, along with their associated uncertainty, are used as covariates on the response variables of interest (e.g., capture probability or survival; Bonner et al. 2010, Schofield and Barker 2011). Bayesian imputation can reveal previously obscured size-dependent relationships (Schofield and Barker 2011, Rose and Todd 2017), and is the best method for modeling time-varying individual covariates when capture probabilities are low (Bonner et al. 2010). Advances in methods for missing covariate data empower us to answer questions about the relationship between body size and survival in elusive species that would have been difficult or impossible to address until recently.

Bayesian imputation could be useful for studies of snake population ecology, which are often hampered by low capture probabilities (Parker and Plummer 1987, Steen 2010). Natricine snakes (family Colubridae, subfamily Natricinae) present good subjects for examining size-dependent survival because individuals rapidly increase in size early in life, and survival often differs between juveniles and adults (Stanford and King 2004, Miller et al. 2011). Body size may be a better predictor of survival rate than age because although growth generally is rapid for young snakes and

slows with age, adults can be highly variable in their maximum body size (King et al. 2016), and mortality due to predation may decrease for the largest individuals (Sparkman et al. 2013). Some species exhibit a unimodal relationship between survival and size (Brown and Weatherhead 1999, Stanford and King 2004), while others may have a positive, linear relationship between survival and size (Hansen et al. 2015). Accurately estimating the shape of the size–survival relationship (e.g., linear vs. unimodal) is especially important for imperiled species, because the shape can influence management strategies derived from demographic models (Easterling et al. 2000, Dahlgren et al. 2011).

Here, we integrate a Bayesian model of somatic growth into a multi-state, hierarchical CMR model to fully account for the uncertainty in an individual's size when it is not captured, and to share information on the capture and survival processes among sites and years. We use this integrated model to estimate survival for the giant gartersnake, *Thamnophis gigas*, an elusive species with low capture probability (Halstead et al. 2013). We sought to answer three key questions for this threatened snake species: (1) Does survival vary as a function of snake body size? (2) How much does survival vary among populations and over time? (3) Is survival related to precipitation, habitat composition, and prey abundance? Our results have implications for the conservation of giant gartersnakes and illustrate the effectiveness of hierarchical Bayesian models for the study of rare and elusive species.

METHODS

Study species

The giant gartersnake is a semi-aquatic species of snake precinctive to the Central Valley of California, USA, where it inhabits canals, sloughs, wetlands, and other slow-moving or stagnant bodies of water (Rossman et al. 1996). Giant gartersnakes eat a variety of fish and amphibians and may prefer native amphibians over other prey types (Ersan 2015). Due to the loss of >90% of their wetland habitat (Huber et al. 2010), the giant gartersnake is listed as threatened under both the state (California Fish and Game Commission 1971) and federal Endangered Species Acts (U.S. Fish and Wildlife Service 1993). Giant

gartersnakes now occur primarily near rice agriculture, as the associated canals provide flooded habitat during much of the snakes' active season (Halstead et al. 2010).

Data collection

We performed CMR studies of giant gartersnakes at 10 sites within the Sacramento Valley, California, USA (Fig. 1). Wetland habitat at our study sites was a mixture of remnant or created lentic wetlands and agricultural canals. Exceptions are Old Natomas North, Old Natomas Central, and Natomas 5, which comprised canals only, and Natomas 4, which comprised wetlands. We collected data from 1999 to 2016, with individual sites sampled from 4 to 11 yr (Table 1). We only used capture data from sites that were consistently sampled year after year for four or more years, although at some sites the position of our trap arrays changed between years to follow the availability of wetland habitat, which could have led to apparent emigration of snakes outside our study area and underestimates of survival. We captured snakes using modified aquatic funnel traps (Casazza et al. 2000, Halstead et al. 2013), set in lines of 50–100 traps along the edges of canals or emergent vegetation in wetlands. At each site, we set 3–5 trap lines, resulting in a total of 150–250 traps per site. We sampled sites between April and September each year, with an average of 71 consecutive days (standard deviation [SD] = 32) of sampling per site, per year. We checked traps daily, processed snakes in the field, and released snakes on the day of capture, except for a small number of snakes that received radio-transmitters as part of a separate study; these snakes were released approximately 7 d after capture. We determined sex and measured the snout–vent length (SVL) of all snakes. We marked snakes by branding ventral scales using a portable medical cautery unit (Winne et al. 2006) and also inserted PIT tags into snakes >30 g mass.

We also collected data on the habitat at each site, including vegetation composition and prey abundance. We estimated the percent cover of emergent vegetation, floating vegetation, submerged vegetation, and terrestrial vegetation within a 1 m radius of every fifth trap, and within 10–20 circular quadrats with a 1 m radius randomly located 2–5 m on either side of every fifth trap along the trap array. Emergent

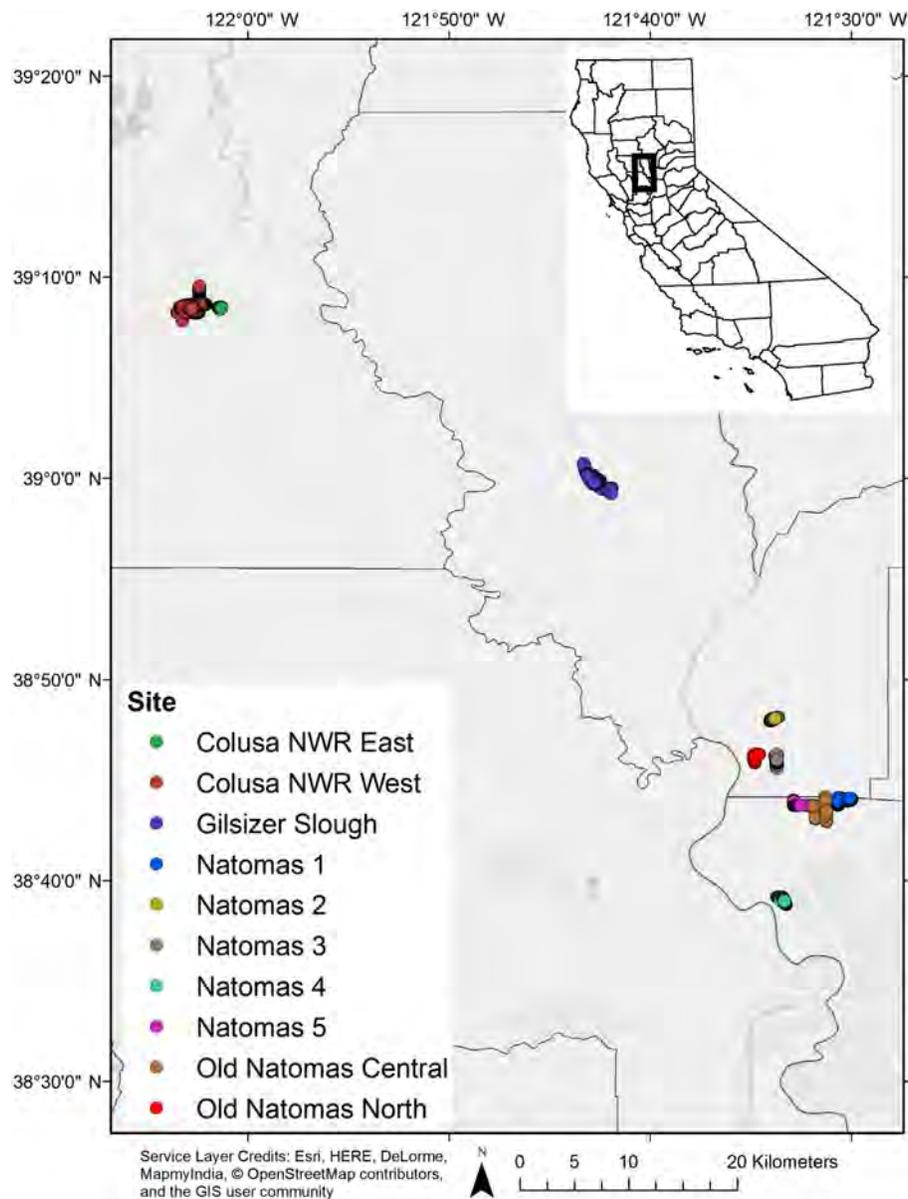


Fig. 1. Location of study sites within the Sacramento Valley, California, USA.

vegetation at our sites included tules (*Schoenoplectus acutus*), cattails (*Typha* spp.), and water-primrose (*Ludwigia* spp.). Floating vegetation comprised mosquito fern (*Azolla* spp.), algae, and duckweed (*Lemna* spp.). Terrestrial vegetation was primarily grasses, weedy dicots, and small shrubs along the edge of wetland habitat. Submerged vegetation comprised coontail (*Ceratophyllum demersum*), milfoil (*Myriophyllum* spp.), and pondweed (*Potamogeton* spp.).

As an index of the prey base available at each site, we counted the number of adult and larval anurans, and the number of fish within every fifth trap. The two anuran species present at our sites are the non-native American bullfrog (*Rana catesbeiana*) and the native Pacific treefrog (*Pseudacris regilla*), both of which are consumed by giant gartersnakes (Ersan 2015). Many small fish that serve as prey for giant gartersnakes are also captured by our traps, including western

Table 1. Summary of years and number of individuals sampled at each site.

Site	Code	Years sampled	Captures	Individuals
Colusa NWR East	COE	2012–2016	152	78
Colusa NWR West	COW	2000–2005, 2012–2016	1357	596
Gilsizer Slough	GI	2007–2016	525	262
Natomas 1	NAT1	2011–2016	538	345
Natomas 2	NAT2	2011–2016	263	166
Natomas 3	NAT3	2011–2016	156	125
Natomas 4	NAT4	2011–2016	13	9
Natomas 5	NAT5	2011–2016	139	84
Old Natomas North	NATN	2000–2003	135	90
Old Natomas Central	NATC	1999–2003	220	136

mosquitofish (*Gambusia affinis*), Mississippi silversides (*Menidia beryllina*), sunfish (*Lepomis* spp.), black basses (*Micropterus* spp.), and other non-native species in the families Cyprinidae, Centrarchidae, and Ictaluridae (Ersan 2015).

Hierarchical Cormack-Jolly-Seber model

We fit a hierarchical, multi-state, robust-design Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) to our CMR data to estimate annual apparent survival (ϕ), temporary emigration (γ''), and daily (re)capture probability (p) at each site, in each year. Our model was based on code developed by Rankin et al. (2016). The robust-design model classifies sampling into widely separated primary periods, between which the population is open, with each primary period composed of multiple secondary periods, between which the population is assumed to be closed (Pollock 1982). The CJS model conditions on first capture, and individuals can occupy one of three states: dead, alive and outside the study area, and alive and inside the study area. Individuals temporarily emigrate from the study area with probability γ'' and stay inside with probability $1 - \gamma''$. Individuals that are outside the study area remain outside with probability γ' and return to the study area with probability $1 - \gamma'$. We summed the number of captures for an individual in a given year and treated this total number of captures as a binomial response, with the number of trials equal to the number of days that a particular site was sampled that year. We included random effects of study site on p , ϕ , and γ'' and nested random effects of year within site on all three parameters. We modeled the probability of an individual staying offsite (γ') as

constant among sites and years, because with CMR data only, it is difficult for the model to estimate variation in this parameter.

We used Bayesian imputation to infer the size of snakes when they were not captured. We adapted code from Schofield and Barker (2011) to implement a time-varying individual covariate in an open population model. We integrated a von Bertalanffy growth model for *Thamnophis gigas* (Rose et al. 2018b) based on the model developed by Eaton and Link (2011) into our hierarchical multi-state CJS model, and used SVL as a measure of snake body size. The integrated growth model imputes a probability distribution for the SVL of a snake when it is not captured, and therefore incorporates uncertainty in this unobserved covariate. We modeled linear (θ_1) and quadratic (θ_2) effects of snake SVL on p , as well as effects of sex (male, θ_3) and trap modifications implemented in 2013 (θ_4) on p , where ω is the intercept on the logit scale (Eq. 1). We modified traps by extending the wide end of funnel openings to guide snakes into the trap and adding cable ties to create a one-way funnel opening that discourages snakes from escaping the trap, once captured (Halstead et al. 2013).

$$\begin{aligned} \text{logit}(p) = & \omega + v_1 \times \theta_1 \times \text{SVL} + v_1 \times v_2 \times \\ & \theta_2 \times \text{SVL}^2 + v_3 \times \theta_3 \times \text{male} \\ & + v_4 \times \theta_4 \times \text{mod} \end{aligned} \quad (1)$$

We used indicator variable selection to estimate support for the inclusion of covariates on p (Kuo and Mallick 1998). In short, each coefficient (θ) is multiplied by a dummy indicator variable (v) that can take on a value of 1 if θ is turned on and 0 if θ is turned off. This binary indicator

variable allows the MCMC sampler to choose whether a covariate effect is included in the model or not, and important covariates will be included in more model iterations (Hooten and Hobbs 2015). Each indicator variable had a Bernoulli (0.5) prior, so most covariates had a 50% prior probability of being included in the model. The quadratic effect of size on p (v_2) could only be turned on if the linear effect (v_1) was also turned on, and thus, v_2 had a 25% prior probability of inclusion (0.5×0.5). We report the posterior probability of each covariate, and for covariates that appear important, we plot model-averaged relationships between the covariate and p .

We compared four survival models representing different hypotheses for the relationship between snake size and survival: (M0) a null model with no relationship between snake size and survival; (M1) a linear size–survival relationship; (M2) a quadratic size–survival relationship; and (M3) a linear size–survival relationship with an asymptote <1 (survival-ceiling model). Survival estimates from radio-tracked adult female giant gartersnakes suggest that survival probability might approach an asymptote near 0.61 for the largest individuals (Halstead et al. 2012). To allow for the size–survival function to asymptote at a probability of survival <1 , M3 includes a survival-ceiling parameter (c). The ceiling parameter is multiplied by the size-dependent survival probability and puts an upper limit on the survival rate (Hobbs and Hooten 2015). For example, if survival exhibits a positive, linear relationship with size, and the ceiling parameter equals 0.8, survival will increase with size and approach a maximum value of 0.8, rather than 1, for the largest individuals.

$$\phi = \frac{1}{1 + \exp(-(\alpha + v_5 \times \beta_3 \times \text{male}))} \quad (\text{M0})$$

$$\phi = \frac{1}{1 + \exp(-(\alpha + \beta_1 \times \text{SVL} + v_5 \times \beta_3 \times \text{male}))} \quad (\text{M1})$$

$$\phi = \frac{1}{1 + \exp(-(\alpha + \beta_1 \times \text{SVL} + \beta_2 \times \text{SVL}^2 + v_5 \times \beta_3 \times \text{male}))} \quad (\text{M2})$$

$$\phi = \frac{c}{1 + \exp(-(\alpha + \beta_1 \times \text{SVL} + v_5 \times \beta_3 \times \text{male}))} \quad (\text{M3})$$

Unlike the indicator variable method used above for covariates of p , we did not want to compare all possible combinations of size covariates on survival, but rather these four mutually exclusive models. We used the product-space method, in which the MCMC sampler can move between alternative models for each iteration, to compare the four size–survival models (Tenan et al. 2014). We used Gibbs Variable Selection to impose pseudo-priors that kept model parameters (e.g., c) within a reasonable range when the corresponding model was turned off (Dellaportas et al. 2002). We first fit models M0–M3 independently to the same data and used the posterior distributions for α , β_1 , β_2 , and c from each model to define pseudo-priors for these parameters. Each model had an equal prior probability (0.25), and we calculated the posterior probability of each model based on the number of MCMC iterations in which that model was selected. We then calculated model-averaged predictions of the size–survival relationship using the posterior probability of each model. The effect of sex on survival (β_3) could be turned on or off for each of the four models using a binary indicator variable (v_5) with a prior probability of 0.5 of being included in the model. All parameters had uninformative or weakly informative priors (Table 2).

We evaluated the goodness-of-fit of our CMR model using a posterior predictive check to calculate a Bayesian P -value. We simulated replicate recapture data with the CMR model and calculated the number of recaptures for each individual snake in the observed and replicate data, as well as the expected number of recaptures based on individual recapture probabilities for each year a snake was available for capture (i.e., alive and on-site). We then calculated the discrepancy between the expected number of recaptures and the observed and replicate number of recaptures using the Freeman-Tukey statistic (Brooks et al. 2000). We visually inspected the discrepancy by plotting the Freeman-Tukey statistic for the observed and replicate data, and we calculated a Bayesian P -value based on the number of

Table 2. CJS model parameters, descriptions, priors, and model-averaged estimates.

Model component	Parameter	Symbol	Prior distribution	Prior values	Mean	SD	2.50%	97.5%
Survival	Mean apparent survival	ϕ	Beta	(1, 1)	0.448	0.079	0.295	0.609
	SD, site random effect on ϕ	$\sigma_{\phi\text{-site}}$	Half-Cauchy	(0, 1)	0.165	0.112	0.029	0.447
	SD, year random effect on ϕ	$\sigma_{\phi\text{-}t}$	Half-Cauchy	(0, 1)	0.165	0.077	0.035	0.341
	Linear size effect on ϕ	β_{SVL}	Normal	(0, 1)	0.753	0.479	0.116	2.028
	Quadratic size effect on ϕ	β_{SVL^2}	Normal	(0, 1)	-0.211	0.210	-0.596	0.000
	Sex effect on ϕ (male)	β_{male}	Normal	(0, 1)	-0.066	0.234	-0.786	0.073
Capture	Survival-ceiling	c	Beta	(1, 1)	0.623	0.070	0.494	0.759
	Mean capture probability	p	Uniform	(0, 1)	0.008	0.002	0.005	0.012
	SD, site random effect on p	$\sigma_{p\text{-site}}$	Half-Cauchy	(0, 1)	0.002	0.002	0.000	0.007
	SD, year random effect on p	$\sigma_{p\text{-}t}$	Half-Cauchy	(0, 1)	0.006	0.002	0.004	0.010
	Linear size effect on p	θ_{SVL}	Normal	(0, 1)	0.074	0.138	-0.214	0.340
	Quadratic size effect on p	θ_{SVL^2}	Normal	(0, 1)	-0.061	0.062	-0.176	0.000
	Sex effect on p (male)	θ_{male}	Normal	(0, 1)	-0.012	0.062	-0.212	0.000
	Trap modification effect on p	θ_{mod}	Normal	(0, 1)	0.327	0.285	0.000	0.868
	Emigration	Probability of staying offsite	γ'	Beta	(1.3, 1.3)	0.548	0.144	0.268
Probability of moving offsite		γ''	Beta	(1, 1)	0.458	0.082	0.290	0.614
SD, site random effect on γ''		$\sigma_{\gamma''\text{-site}}$	Half-Cauchy	(0, 1)	0.082	0.067	0.003	0.249
SD, year random effect on γ''		$\sigma_{\gamma''\text{-}t}$	Half-Cauchy	(0, 1)	0.125	0.071	0.008	0.283
Growth	Asymptotic length (female)	L_{∞}	Normal	(910.6, 20.5)	894	12.3	866	909
	Male effect on L_{∞}	$m_{L_{\infty}}$	Normal	(-216.3, 14.7)	-221	10.0	-238	-198
	Growth coefficient (female)	k	Normal	(1.308, 0.241)	1.740	0.051	1.638	1.835
	Male effect on k	m_k	Normal	(0.296, 0.143)	0.514	0.071	0.372	0.651

Notes: CJS, Cormack-Jolly-Seber; SD, standard deviation. Normal distributions are defined by their mean and SD, half-Cauchy distributions by the location and scale, beta distributions by the two shape parameters (α and β), and the uniform distribution by the lower and upper limits. Standard deviation parameters for random effects have been converted back to the probability scale using the delta method (Kéry and Schaub 2012). Estimates are weighted averages from four multi-state CJS models with all capture-mark-recapture data collected from 10 sites from 1999 to 2016.

iterations in which the discrepancy for the replicate data was greater than that for the observed data. Bayesian P -values near 0.5 indicate good fit, while values near 0 or 1 are evidence that the model does not fit the observed data (Kéry and Schaub 2012). There was no evidence of a lack of fit for our CMR model, and the Bayesian P -value was 0.4.

Environmental covariates

To evaluate the importance of environmental variables, we fit a second CJS model that included annual precipitation, prey abundance (fish, frogs, and tadpoles), and habitat composition at each site as covariates. This second CJS model was fit to CMR data collected at Natomas 1–5, Colusa NWR West, Colusa NWR East, and Gilsizer Slough from 2011 to 2016, because those were the sites and years from which we had data on prey abundance and habitat composition. Annual precipitation for year t is the amount of precipitation that fell during the water year from

1 October in year $t - 1$ to 30 September in year t . We calculated annual precipitation from the PRISM climatic database (PRISM Climate Group 2016) and included both precipitation in the previous water year ($t - 1$) and precipitation in the current water year (t) as covariates on survival. We summarized prey abundance with three covariates representing the capture rate of fish, adult anurans (frogs), and larval anurans (tadpoles) at each site, in each year. The capture rate of prey was calculated using a zero-inflated Poisson model implemented in Stan (Carpenter et al. 2017), which shares information among sites and years to provide better estimates for small samples (see Rose et al. 2018b for details of this model). Habitat composition covariates included the average percent cover of emergent, terrestrial, floating, and submerged vegetation at each site, in each year. We tested for the importance of environmental covariates on survival using the indicator variable selection method described above for covariates of p (Kuo and Mallick 1998).

We estimated the effects of environmental covariates on survival for the two top-ranking size–survival models.

We fit our CMR models in JAGS (version 4.2.0; Plummer 2003), accessed through R (version 3.3.1; R Core Team 2016) using the runjags package (version 2.0.4-2; Denwood 2016). We standardized all covariates (including snake SVL) to have a mean of zero and SD of one to improve the efficiency of the MCMC sampler and make interpretation of model coefficients easier. We ran the CJS models on 20 chains for 10,000 sampling iterations (20,000 for the environmental covariates model) after an adaptation period of 2000 iterations and a burn-in of 2000 iterations. Model code and data are available in Data S1. We evaluated mixing and convergence of chains by inspecting trace plots and calculating the \hat{R} statistic (Brooks and Gelman 1998); we found no evidence of lack of convergence. For random effects parameters, we present SDs on the probability scale, by using the delta method to transform from the logit scale (Kéry and Schaub 2012). We divided the SD of a random effect (e.g., the effect of site on p) by the mean value of that parameter (e.g., mean p) to calculate the relative magnitude of random effects. We present posterior means and symmetric 95% credible intervals for all parameters unless specified otherwise.

RESULTS

Capture data summary

We made 3498 captures of 1891 individuals over the 17 yr of study. The sex ratio of captured

snakes from all sites was 1.2 females:1 male; 1015 individuals were female, 847 were male, and 29 were of unknown sex. The largest number of individuals were captured at Colusa NWR West, followed by Natomas 1 and Gilsizer Slough (Table 1). Of 1891 captured individuals, 1658 were only captured in one year, 187 were captured in two years, 37 were captured in three years, and nine were captured in four years. The longest interval between the first and last capture of a snake was 10 yr, but the majority of recaptured snakes were recaptured one year (63% of recaptures) or two years (25%) after their most recent capture. Within a year, individuals were captured from 1 to 30 times (mean number of captures given a snake was captured once = 1.6, SD = 1.5).

CJS survival model

Females reached greater lengths ($L_{\infty} = 894$ mm, 866–909) than males ($L_{\infty} = 673$, 656–688), and males approached their asymptotic length faster ($k = 2.25$, 2.08–2.40) than females ($k = 1.74$, 1.64–1.84; Table 2). For more results from the growth model, please see Rose et al. (2018b).

There was strong support for size-dependent capture probability, with a linear size effect included in 100% of model iterations and a quadratic effect in 57% of iterations (Table 3). Capture probability exhibited a unimodal relationship with size, with the highest capture probability for individuals between 500 and 900 mm SVL. There was high uncertainty in the capture probability of snakes <400 mm SVL or >800 mm SVL (Fig. 2a). There was no support for a sex difference in capture probability. Capture probability

Table 3. The top six models (posterior probability ≥ 0.05) for the capture probability and survival of giant garter-snakes from 10 sites in the Sacramento Valley sampled from 1999 to 2016.

Survival model	θ_{SVL}	$\theta_{\text{SVL}2}$	θ_{male}	θ_{mod}	β_{SVL}	$\beta_{\text{SVL}2}$	c	β_{male}	Posterior probability
M2	1	1	0	1	1	1	0	0	0.169
M2	1	0	0	1	1	1	0	0	0.127
M3	1	1	0	1	1	0	1	0	0.098
M3	1	0	0	1	1	0	1	0	0.090
M2	1	1	0	0	1	1	0	0	0.081
M3	1	0	0	0	1	0	1	0	0.054
Pr(Included)	1	0.571	0.072	0.692	0.991	0.560	0.377	0.185	—

Notes: Each row represents a different model, and the rightmost column is the posterior probability of that model being chosen. The bottom row shows the posterior probability of individual covariates being included in the model, based on the number of model iterations in which that covariate effect was included. θ represents a covariate on p , and β represents a covariate on ϕ .

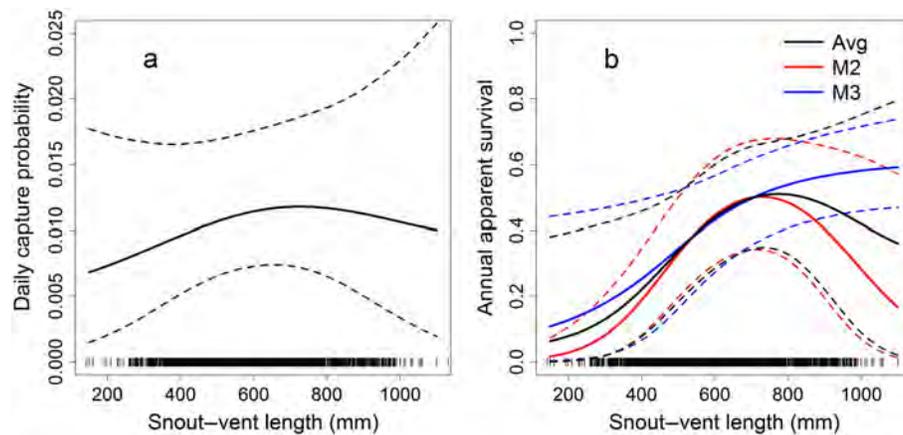


Fig. 2. Relationships between snake size and (a) capture probability (p) and (b) apparent survival (ϕ) for females. Black lines represent model-averaged relationships. In panel b, the red lines represent the quadratic model (M2), and the blue lines represent the survival-ceiling model (M3). Solid lines represent the mean predicted relationship, and dashed lines are 95% credible intervals. Vertical dashes along the x-axis represent the sizes of captured snakes.

was higher after trap modifications were implemented (Table 2). Even after accounting for the effect of trap modifications, there was a large amount of variation in capture probability attributable to site and year. The variation in daily capture probability among years (SD = 0.0064, 95% Credible Interval = 0.0037–0.0101) was larger than variation among sites (SD = 0.0025, 0.0001–0.0070). Variation in both space and time was substantial: The SD of the year random effect on capture probability was 77% (59–99%) of the mean, while the SD of the site random effect was 30% (1–77%) of the mean.

There was also clear support for size-dependent survival. Survival probability increased with snake size, up to a peak, after which survival declined slightly (Fig. 2b). Survival model M2, with linear and quadratic effects of size on survival, had the most support and was chosen in 56% of iterations, including the two top-ranked models. There was slightly weaker support for the survival-ceiling model (M3), which was chosen in 38% of iterations, followed by the linear size–survival model (M1), which was only chosen in 5% of iterations (Table 3). The combination of these parameter effects on survival is illustrated by looking at the model-averaged relationship between snake size and survival. The model-averaged survival curve showed an initial increase in survival probability with size,

going from a survival rate of <0.2 for snakes under 400 mm SVL to a peak survival rate of 0.51 for snakes near 800 mm SVL, beyond which survival decreased slightly with increasing size on average (Fig. 2b). There was substantial uncertainty around the size–survival relationship for small (<400 mm SVL) and very large (>800 mm SVL) snakes, but the two top models (M2 and M3) made similar predictions for snakes of intermediate size (Fig. 2b). There was little support for sex differences in survival (Table 3).

The average annual apparent survival probability varied over time and among sites (Figs. 3–5). The average survival rate was highest at Colusa NWR West ($\phi = 0.59$, 0.47–0.73) and lowest at Natomas 1 ($\phi = 0.35$, 0.17–0.56) and Natomas 5 ($\phi = 0.36$, 0.14–0.59; Fig. 3). The variation in survival among sites (SD = 0.165, 0.029–0.447) and years (SD = 0.165, 0.035–0.341) was similar and was approximately 32% (5–82%) and 32% (6–64%) of the average annual survival, respectively.

Snakes had a nearly equal annual probability of remaining on-site or temporarily emigrating offsite, with the mean value of γ'' equal to 0.46 (Table 2). The variation in temporary emigration among years (SD = 0.125, 0.008–0.283) was 29% (2–74%) of the mean temporary emigration probability, and the variation among sites (SD = 0.082, 0.003–0.249) was 19% (1–65%) of the mean value of γ'' .

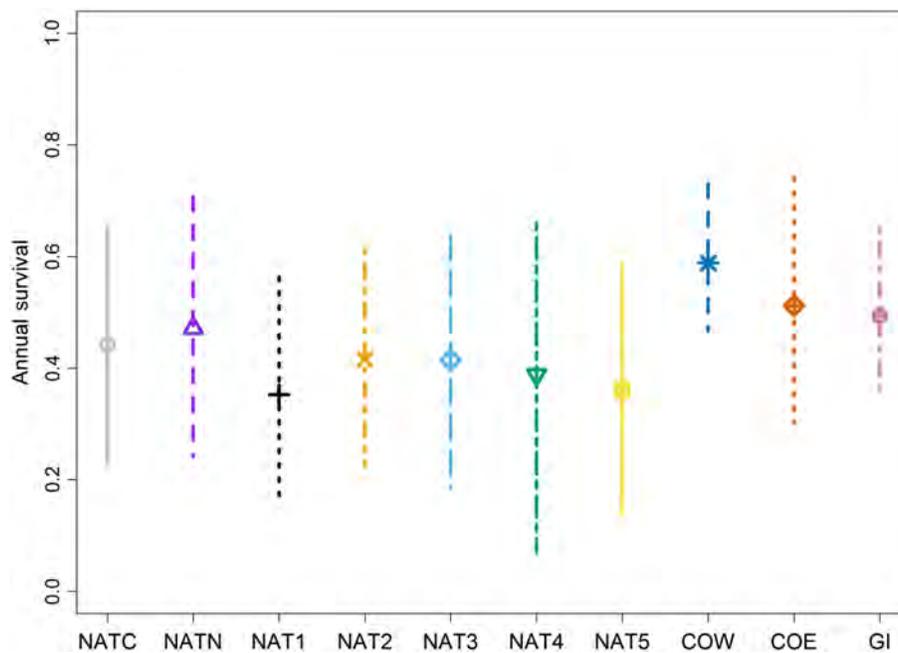


Fig. 3. Average annual apparent survival probability, ϕ , for each study site. Points represent posterior means, and lines are 95% credible intervals.

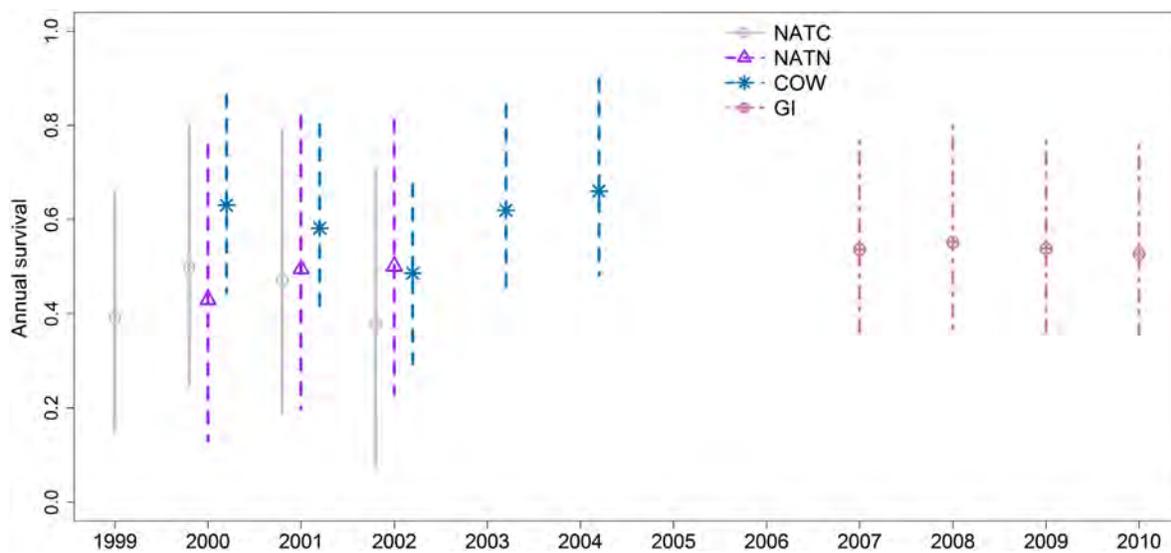


Fig. 4. Annual apparent survival probability, ϕ , by site for 1999–2010. Points represent posterior means, and lines are 95% credible intervals.

Environmental covariates of survival

Our dataset for estimating the effects of environmental covariates on survival comprised 2204 captures of 1244 snakes at eight sites from 2011 to

2016. The importance of environmental covariates was qualitatively similar for both of the top-ranking size–survival models (M2 and M3); for brevity, we only present the results for model M2 (linear

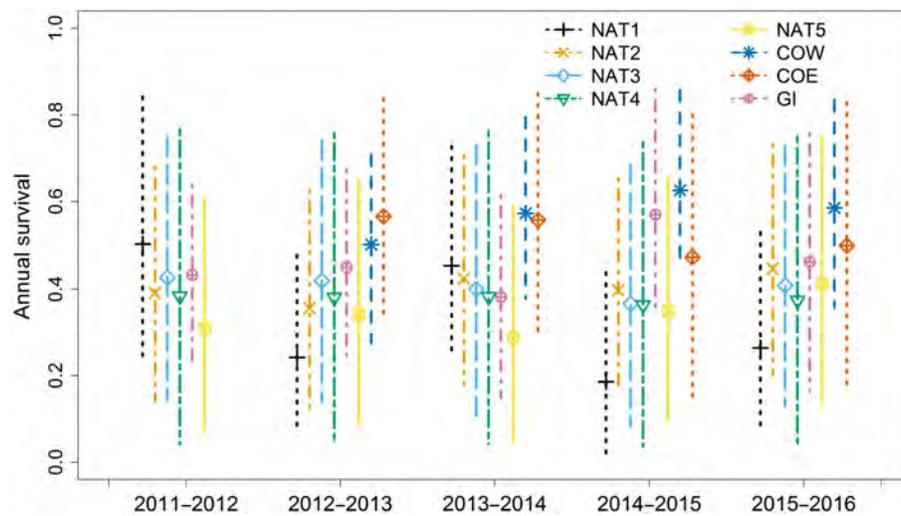


Fig. 5. Annual apparent survival probability, ϕ , by site for 2011–2015. Points represent posterior means, and lines are 95% credible intervals.

and quadratic effects of size on survival). Floating vegetation cover, emergent vegetation cover, and precipitation in the previous year had the strongest relationships with survival, as these covariates were included in >75% of model iterations (Table 4). All other environmental covariates were included in <50% of model iterations. The top-ranked model included effects of emergent vegetation cover, floating vegetation cover, precipitation in the previous year, and fish abundance

on annual survival. The precipitation that fell at a site in the previous water year ($\beta_{ppt,t-1} = 0.588$, 0.067–1.24; $\text{Pr}(\text{inclusion}) = 0.77$) and the proportions of emergent ($\beta_{ev} = 0.944$, 0.292–1.74; $\text{Pr}(\text{inclusion}) = 0.95$) and floating ($\beta_{fv} = 0.773$, 0.139–1.51; $\text{Pr}(\text{inclusion}) = 0.86$) vegetation cover were all positively related to survival (Table 4; Fig. 6). It is important to note that although the observed cover of emergent vegetation at a site ranged from 0% to 78%, the majority of sites (42/

Table 4. Parameter estimates for environmental covariates on survival from the Cormack-Jolly-Seber model on capture–mark–recapture data collected from 2011 to 2016.

Model component	Parameter	Symbol	Mean	SD	Percentile		$P(\text{in})$	f
					2.50%	97.50%		
Survival	Mean apparent survival	ϕ	0.362	0.115	0.165	0.599	—	—
	SD, site random effect on ϕ	$\sigma_{\phi-\text{site}}$	0.079	0.074	0.003	0.272	—	—
	SD, year random effect on ϕ	$\sigma_{\phi-t}$	0.161	0.108	0.008	0.424	—	—
	Precip (year $t - 1$) effect on ϕ	$\beta_{ppt, t-1}$	0.588	0.296	0.067	1.237	0.772	0.986
	Precip (year t) effect on ϕ	$\beta_{ppt,t}$	0.103	0.435	−0.740	1.006	0.292	0.592
	Fish abundance effect on ϕ	β_{fish}	0.365	0.241	−0.083	0.875	0.462	0.947
	Frog abundance effect on ϕ	β_{frog}	0.149	0.508	−0.856	1.190	0.332	0.618
	Tadpole abundance effect on ϕ	β_{tad}	−0.071	0.398	−0.896	0.669	0.279	0.556
	Emergent vegetation effect on ϕ	β_{ev}	0.944	0.365	0.292	1.737	0.946	0.998
	Terrestrial vegetation effect on ϕ	β_{tv}	0.024	0.324	−0.706	0.604	0.228	0.562
	Floating vegetation effect on ϕ	β_{fv}	0.773	0.349	0.139	1.513	0.856	0.991
	Submerged vegetation effect on ϕ	β_{sv}	0.090	0.224	−0.411	0.489	0.202	0.688

Notes: SD, standard deviation. For environmental covariates, the parameter estimates and their summary statistics are based on model iterations where that parameter was included in the model. $P(\text{in})$ represents the probability of that environmental covariate being included in the model. f represents the proportion of the posterior distribution that has the same sign as the mean. Parameters with 95% credible intervals that do not overlap zero are in bold.

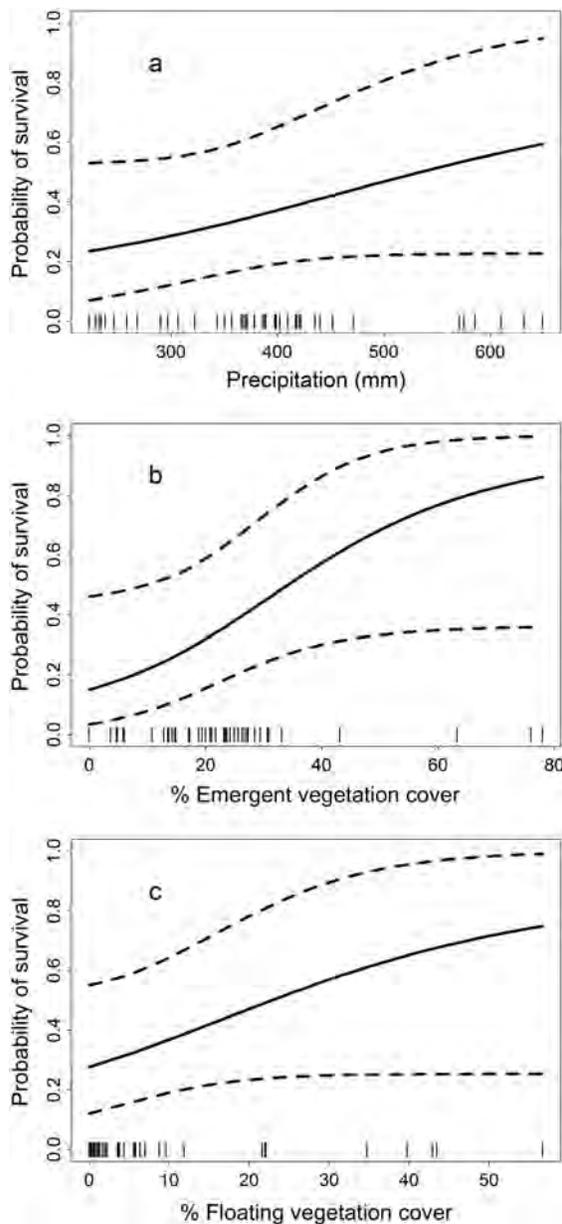


Fig. 6. Relationship between snake apparent survival and (a) precipitation in the previous water year, (b) % cover of emergent vegetation, and (c) % cover of floating vegetation. Solid lines represent posterior mean relationships, and dashed lines are 95% credible intervals. Vertical dashes along the x -axis indicate observed values for the precipitation and emergent and floating vegetation covariates.

46) had <35% emergent vegetation cover each year. Similarly, for floating vegetation cover, the majority of sites (37/46) had <20% floating vegetation cover each year (Fig. 6). When environmental covariates were included in the model, the variation in survival among years ($\sigma_{\phi-t}$) was larger than variation among sites ($\sigma_{\phi-site}$; Table 4).

DISCUSSION

Integrating an individual growth model with a hierarchical, multi-state CMR model in a Bayesian framework enabled us to estimate the relationship between size and survival in a threatened, elusive species. We found that survival is positively related to individual size in giant gartersnakes up to a peak, after which survival may decrease or remain constant for the largest individuals. Even for large snakes with peak survival probability, the mean annual survival rate in our study was only approximately 51%, which indicates this species is short-lived with high population turnover. The quadratic size–survival relationship in this study differs from strictly positive linear size–survival relationship found in the only comparable study for giant gartersnakes (Hansen et al. 2015). Because we used a hierarchical model, we were able to obtain site- and year-specific estimates of survival and capture probability, while estimating many fewer parameters than if we had treated site and year as fixed effects. Survival varied substantially among both sites and among years within a site, and some of this variation was attributable to differences in precipitation and vegetation composition. Capture data were sparse at some sites, and we would have been unable to obtain year-specific estimates of survival if we had analyzed data from each site separately, rather than in a hierarchical model.

While the two top-ranked models predict similar relationships between snake size and survival for snakes between 400 and 800 mm SVL, they differ in whether survival declines or remains constant for the largest snakes. The uncertainty in the size–survival relationship for large adult snakes is likely because we had few recaptures of

the largest individuals, as capture probabilities were low for snakes >800 mm SVL. The limited number of recaptures reduces the precision with which we can estimate survival, and likely resulted in model selection uncertainty between a quadratic size–survival curve and a linear size–survival curve with an upper asymptote (survival-ceiling) near 0.62, and our model-averaged curve incorporates both of these possibilities. Survival is likely relatively constant for female snakes >800 mm SVL. A radio-telemetry study of large adult female giant gartersnakes, ranging from 648 to 1040 mm SVL (mean = 834 mm), found that the average annual survival rate of adult females was 0.61, with no support for an effect of snake SVL on survival (Halstead et al. 2012). Elucidating whether survival declines with size for large adult female giant gartersnakes would require larger samples of this life stage, which may be better studied using radio-telemetry than mark–recapture.

Estimating the survival rate of neonate reptiles is notoriously challenging (Parker and Plummer 1987, Pike et al. 2008). Our size–survival curves predict very low survival for small snakes during their first year of life, but we captured few snakes <300 mm SVL, and consequently, there is great uncertainty in the survival of this size class. We make many more captures of snakes that are ~1 yr old and ≥400 mm SVL (Rose et al. 2018b). Consequently, we have greater confidence in our estimates of annual survival for snakes >400 mm SVL than for very small neonates. Some studies of natricine snakes have estimated the survival of neonates during their first year by releasing marked, captive-born neonates and recording the number recaptured or re-sighted the following year. A study of *Thamnophis sirtalis fitchi* estimated first-year survival to be 0.29 (Jayne and Bennett 1990), and a study of *Nerodia sipedon* estimated neonate survival was 0.31 from birth to emergence the following spring (Kissner and Weatherhead 2005). Given the difficulty of capturing neonate giant gartersnakes, future demographic modeling efforts would be well served to model recruitment as the addition of 1-yr-old snakes into the population, because that is the age/size at which we can reliably begin tracking the growth, survival, and maturity of snakes. Nevertheless, designing studies to better quantify the first-year survival of giant gartersnakes

might be important for understanding what drives variation in recruitment of 1-yr-old snakes among sites and years. Specifically, it would be valuable to quantify the relative contributions of variation in female fecundity and variation in neonate survival to variation in recruitment over space and time.

The size dependence of survival, and spatial and temporal variation in survival among giant gartersnake populations, is similar to patterns observed in other gartersnake species. Survival varied over time and among ecotypes of the western terrestrial gartersnake, *Thamnophis elegans*, in northern California, with size-dependent survival observed in some populations (Miller et al. 2011). A long-term study of the plains gartersnake, *Thamnophis radix*, found that survival was sex- and age-dependent; mean survival estimates ranged from 0.16 for neonate snakes to peaks of 0.52 and 0.42 for two-year-old females and males, after which survival declined for snakes ≥3 yr old (Stanford and King 2004). In contrast, survival was sex- but not age-dependent in a population of the aquatic gartersnake, *Thamnophis atratus*, in northern California, with females (0.64) having higher annual survival than males (0.56; Lind et al. 2005). Annual survival of the semi-aquatic natricine *N. sipedon* in two populations in Ontario, Canada, also exhibited a unimodal relationship with size, with similar mean survival estimates (0.53–0.58) to those for giant gartersnakes in this study (Brown and Weatherhead 1999). Given that natricine snakes generally exhibit female-biased sexual size dimorphism (Shine 1994), it is possible that previous studies that found sex differences in survival, but did not include individual size as a covariate, were confounding the effects of sex and size. Likewise, given that individual snakes can vary in their maximum length (King et al. 2016), disentangling the importance of age and size on survival is only possible if both are included in the same model.

The variation in annual survival of giant gartersnakes among our study populations and over time, and the inter- and intra-specific variation in survival seen in other natricine snakes highlight the importance of long-term, multi-population studies for quantifying natural variation in this key vital rate. Survival estimates from a closely related species, a nearby population of the same species, or from the same population

within a narrow period of time are unlikely to accurately predict annual survival in a given population of a focal species. The amount of natural variation in survival in giant gartersnakes and other natricine snakes demonstrates that demographic population models should not rely solely on mean estimates, but rather include spatial and temporal variation in survival in a stochastic framework.

In addition to the relationship between survival and snake size, we also found survival of giant gartersnakes was positively related to the cover of emergent and floating vegetation. Radio-telemetry studies show that giant gartersnakes select areas with higher cover of emergent vegetation, and occupancy studies show that snakes primarily occur in or near areas that were historically tule marsh (Halstead et al. 2014, 2016). Thus, it is intuitive that snakes survive at a higher rate in habitats that have more emergent vegetation cover, which better replicate the tule marshes these snakes inhabited before widespread land use change. We caution that the positive relationships between emergent and floating vegetation cover and snake survival may not extend to sites with >40% cover of these vegetation types. Giant gartersnakes likely need a mix of vegetation and open water in which to forage (Valcarcel 2011), and wetland habitats that are choked with emergent and/or floating vegetation are likely suboptimal for giant gartersnakes.

For a semi-aquatic snake in a Mediterranean climate, our finding that survival was positively related to the amount of precipitation that falls in the preceding water year is not surprising. Although the precipitation covariate had a lower probability of being included in the model compared to the emergent and floating vegetation covariates, the positive relationship between precipitation and survival was clear. Giant garter-snake growth is also positively related to precipitation (Rose et al. 2018b). In the Sacramento Valley, rainfall is minimal from May through September, which comprises the majority of the active season for giant gartersnakes. The annual survival of giant gartersnakes is thus most influenced by the amount of precipitation that falls from 1 October through 30 April. Because giant gartersnakes now primarily inhabit canals associated with rice agriculture (Halstead et al. 2010), the relationship between precipitation and

survival may be more complex, as both the amount and timing of precipitation locally, and at higher elevations upstream, can influence water management practices at a site. A previous study reported a negative relationship between the survival of *Thamnophis gigas* and the amount of precipitation that fell between 15 April and 15 May; high precipitation during this period can delay rice planting, which affects the condition of canal habitat (Hansen et al. 2015). Our analysis of environmental covariate effects on survival was centered on a period of extreme drought (2012–2015; Robeson 2015). If, as predicted, California experiences more frequent droughts in the future due to anthropogenic climate change (Diffenbaugh et al. 2015), the survival rate of giant gartersnakes might decline as a result.

Estimating survival from wild populations is complicated by the movement of individuals out of the study area. Temporary emigration of individuals from the sampled area leads to negatively biased estimates of apparent survival unless it is explicitly included in a CMR model (Kendall et al. 1997). We accounted for temporary emigration by using a multi-state model in which individuals that were not recaptured could take on one of three states: (1) alive, on-site, but uncaptured, (2) alive and offsite, and (3) dead. Even though we modeled the temporary emigration process, we possibly underestimated true survival, because individuals could permanently emigrate from the study area, and in a few cases, trap arrays were moved between years to follow the availability of aquatic habitat. Our apparent survival estimate, ϕ , is the product of true survival, S , and the probability that an individual does not permanently emigrate from the site. We could potentially improve our estimates of emigration and survival by using auxiliary data on the movement and survival of giant gartersnakes from radio-telemetry studies (Halstead et al. 2012, Reyes et al. 2017) to inform the probability that an individual moves off of the sample array (using a model similar to Powell et al. 2000). Large, adult giant gartersnakes exhibit site fidelity, with small home ranges that overlap between years for most individuals (Reyes et al. 2017). The site fidelity of radio-tracked giant gartersnakes suggests that permanent emigration might not have had a large effect on our estimates of apparent survival for large, adult

snakes. It is possible that site fidelity is weaker in juvenile giant gartersnakes resulting in biased estimates of survival for small individuals, but we lack movement data for this life stage. Another approach would be to use a spatial capture–recapture model, which estimates the movement of individuals on and off of the sampling array based on the locations where an individual is captured (Ergon and Gardner 2014). Spatial capture–recapture requires repeated, spatially distinct captures of individuals within a primary period to estimate their activity center and movement pattern (Royle et al. 2014). Given the low capture probabilities for individual giant gartersnakes, spatial capture–recapture models may not be feasible for this elusive species.

Although our study was focused on individual size as a covariate of survival, our methods can be applied to any number of individual traits that vary over time. Any individual trait could be included as a covariate in a Bayesian CMR model, provided a good model is available to predict how that trait changes over time in the study population. For example, some CMR models have included disease state (e.g., infected or uninfected) as a partially observed covariate (Conn and Cooch 2009, Schofield and Barker 2011). Other time-varying covariates of survival and capture probability could include body mass/condition (Naef-Daenzer et al. 2001, Harding et al. 2011), breeding status (Sandercock et al. 2000), and spatial location or habitat type (Low et al. 2010). For any of these time-varying covariates, Bayesian imputation propagates uncertainty in the covariate to estimates of key vital rates and enables researchers to include data from all individuals in their models, rather than restrict their analysis to a smaller subset of complete cases. We believe Bayesian imputation can empower researchers to include time-varying individual covariates in CMR models, and will be especially useful for taxa with low probabilities of sighting or capture.

CONCLUSIONS

We found that survival increases with body size (SVL) in giant gartersnakes up to a peak, after which their survival rate may decrease slightly or remain constant. This life-history pattern has potential ramifications for the conservation of this threatened species. The relatively low annual

survival rate of large adults suggests few females will survive to reach very large body sizes and produce large litters (Rose et al. 2018a, b), and emphasizes the importance of management actions that could increase the survival of large adult females with high reproductive value. The survival of giant gartersnakes was positively related to the cover of emergent and floating vegetation within wetlands, which provides managers valuable information on how to improve wetland habitats for this species. Survival was also positively related to precipitation, and future studies could investigate how the interaction between precipitation and water availability in managed habitats affects giant gartersnakes. Our results provide much-needed information on the demography of this threatened species and further our understanding of life-history variation in the genus *Thamnophis*. Our study demonstrates the power and flexibility of Bayesian hierarchical models for estimating the survival of elusive species, and the effect of individual and environmental covariates on survival and detection. This study indicates that wider application of hierarchical models to the study of rare and elusive species would improve researchers' ability to extract the most information from available data.

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LITERATURE CITED

Altwegg, R., S. Dummermuth, B. R. Anholt, and T. Flatt. 2005. Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles. *Oikos* 110:55–66.

- Anderson, J. T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science* 8:55–66.
- Blums, P., J. D. Nichols, J. E. Hines, M. S. Lindberg, and A. Mednis. 2005. Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. *Oecologia* 143:365–376.
- Bonner, S. J., B. J. T. Morgan, and R. King. 2010. Continuous covariates in mark-recapture-recovery analysis: a comparison of methods. *Biometrics* 66:1256–1265.
- Brooks, S. P., E. A. Catchpole, and B. J. T. Morgan. 2000. Bayesian animal survival estimation. *Statistical Science* 15:357–376.
- Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- Brown, G. P., and P. J. Weatherhead. 1999. Demography and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. *Canadian Journal of Zoology* 77:1358–1366.
- California Fish and Game Commission. 1971. California code of regulations: animals of California declared to be endangered or threatened 14 CCR 670.5.
- Carpenter, B., A. Gelman, M. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. A. Brubaker, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. *Journal of Statistical Software* 76:1–32.
- Casazza, M. L., G. D. Wylie, and C. J. Gregory. 2000. A funnel trap modification for surface collection of aquatic amphibians and reptiles. *Herpetological Review* 31:91–92.
- Conn, P. B., and E. G. Cooch. 2009. Multistate capture–recapture analysis under imperfect state observation: an application to disease models. *Journal of Applied Ecology* 46:486–492.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- Dahlgren, J. P., M. B. García, and J. Ehrlén. 2011. Non-linear relationships between vital rates and state variables in demographic models. *Ecology* 92: 1181–1187.
- Dellaportas, P., J. J. Forster, and I. Ntzoufras. 2002. On Bayesian model and variable selection using MCMC. *Statistics and Computing* 12:27–36.
- Denwood, M. J. 2016. runjags: an R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. *Journal of Statistical Software* 71:1–25.
- Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences USA* 112:3931–3936.
- Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. *Ecology* 81:694–708.
- Eaton, M. J., and W. L. Link. 2011. Estimating age from recaptured data: integrating incremental growth measures with ancillary data to infer age-at-length. *Ecological Applications* 21:2487–2497.
- Ergon, T., and B. Gardner. 2014. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data. *Methods in Ecology and Evolution* 5:1327–1336.
- Ersan, J. S. M. 2015. Diet and prey preference of giant gartersnakes (*Thamnophis gigas*) in the Sacramento Valley of California. Thesis. California State University, East Bay, Hayward, California, USA.
- Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: A case of environmental canalization? *Ecology* 84:3294–3306.
- Gelman, A., and J. Hill. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, New York, New York, USA.
- Halliday, T., and P. Verrell. 1988. Body size and age in amphibians and reptiles. *Journal of Herpetology* 22:253–265.
- Halstead, B. J., P. Valcarcel, G. D. Wylie, P. S. Coates, M. L. Casazza, and D. K. Rosenberg. 2016. Active season microhabitat and vegetation selection by giant gartersnakes associated with a restored marsh in California. *Journal of Fish and Wildlife Management* 7:397–407.
- Halstead, B. J., G. D. Wylie, and M. L. Casazza. 2010. Habitat suitability and conservation of the giant gartersnake (*Thamnophis gigas*) in the Sacramento Valley of California. *Copeia* 2010:591–599.
- Halstead, B. J., G. D. Wylie, and M. L. Casazza. 2013. Efficacy of trap modifications for increasing capture rates of aquatic snakes in floating aquatic funnel traps. *Herpetological Conservation and Biology* 8:65–74.
- Halstead, B. J., G. D. Wylie, and M. L. Casazza. 2014. Ghost of habitat past: Historic habitat affects the contemporary distribution of giant garter snakes in a modified landscape. *Animal Conservation* 17:144–153.
- Halstead, B. J., G. D. Wylie, P. S. Coates, P. Valcarcel, and M. L. Casazza. 2012. Bayesian shared frailty models for regional inference about wildlife survival. *Animal Conservation* 15:117–124.

- Hansen, E. C., R. D. Scherer, G. C. White, B. G. Dickson, and E. Fleishman. 2015. Estimates of survival probability from two populations of giant garter snakes in California's Great Central Valley. *Copeia* 103:1026–1036.
- Harding, A. M. A., et al. 2011. Adverse foraging conditions may impact body mass and survival of a high Arctic seabird. *Oecologia* 167:49–59.
- Hobbs, N. T., and M. B. Hooten. 2015. Bayesian models: a statistical primer for ecologists. Princeton University Press, Princeton, New Jersey, USA.
- Hooten, M. B., and N. T. Hobbs. 2015. A guide to Bayesian model selection for ecologists. *Ecological Monographs* 85:3–28.
- Huber, P. R., S. E. Greco, and J. H. Thorne. 2010. Boundaries make a difference: the effects of spatial and temporal parameters on conservation planning. *Professional Geographer* 62:409–425.
- Hyslop, N. L., D. J. Stevenson, J. N. Macey, L. D. Carlike, C. L. Jenkins, J. A. Hostetler, and M. K. Oli. 2012. Survival and population growth of a long-lived threatened snake species, *Drymarchon couperi* (Eastern Indigo Snake). *Population Ecology* 54:145–156.
- Jayne, B. C., and A. F. Bennett. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204–1229.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563–578.
- Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, Massachusetts, USA.
- King, R. B., K. M. Stanford, P. C. Jones, and K. Bekker. 2016. Size matters: individual variation in ectotherm growth and asymptotic size. *PLoS ONE* 11:e0146299.
- Kissner, K. J., and P. J. Weatherhead. 2005. Phenotypic effects on survival of neonatal northern water snakes *Nerodia sipedon*. *Journal of Animal Ecology* 74:259–265.
- Kuo, L., and B. Mallick. 1998. Variable selection for regression models. *Sankhya Series B* 60:65–81.
- Lind, A. J., H. H. Welsh, and D. A. Tallmon. 2005. Garter snake population dynamics from a 16-year study: considerations for ecological monitoring. *Ecological Applications* 15:294–303.
- Low, M., D. Arlt, S. Eggers, and T. Pärt. 2010. Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. *Journal of Animal Ecology* 79:214–224.
- Miller, D. A., W. R. Clark, S. J. Arnold, and A. M. Bronikowski. 2011. Stochastic population dynamics in populations of western terrestrial garter snakes with divergent life histories. *Ecology* 92:1658–1671.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730–738.
- Papadatou, E., et al. 2012. Comparing survival among species with imperfect detection using multilevel analysis of mark-recapture data: a case study on bats. *Ecography* 35:153–161.
- Parker, W. S., and M. V. Plummer. 1987. Population ecology. Pages 253–301 in R. A. Seigel, J. T. Collins and S. S. Novak, editors. *Snakes: ecology and evolutionary biology*. Blackburn Press, Caldwell, New Jersey, USA.
- Pike, D. A., L. Pizzatto, B. A. Pike, and R. Shine. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* 89:607–611.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In K. Hornik, F. Leisch, and A. Zeileis, editors. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, Vienna, Austria, March 20–22, 2003.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:3–97.
- Powell, L. A., M. J. Conroy, J. E. Hines, J. D. Nichols, and D. G. Krentz. 2000. Simultaneous use of mark-recapture and radiotelemetry to estimate survival, movement, and capture rates. *Journal of Wildlife Management* 64:302–313.
- PRISM Climate Group. 2016. PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA. <http://prism.oregonstate.edu>
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rankin, R. W., K. E. Nicholson, S. J. Allen, M. Krützen, L. Bejder, and K. H. Pollock. 2016. A full-capture hierarchical Bayesian model of Pollock's Closed Robust Design and application to dolphins. *Frontiers in Marine Science* 3:1–18.
- Rees, M., and S. P. Ellner. 2009. Integral projection models for populations in temporally varying environments. *Ecological Monographs* 79:575–594.

- Reyes, G. A., et al. 2017. Behavioral response of giant gartersnakes (*Thamnophis gigas*) to the relative availability of aquatic habitat on the landscape. U. S. Geological Survey Open-File Report 2017-1141. U. S. Geological Survey, Western Ecological Research Center, Sacramento, California, USA.
- Rivot, E., and E. Prévost. 2002. Hierarchical Bayesian analysis of capture-mark-recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1768–1784.
- Robeson, S. M. 2015. Revisiting the recent California drought as an extreme value. *Geophysical Research Letters* 42:6771–6779.
- Rose, J. P., J. S. M. Eersman, G. D. Wylie, M. L. Casazza, and B. J. Halstead. 2018a. Reproductive frequency and size-dependence of fecundity in the giant gartersnake (*Thamnophis gigas*). *Herpetological Conservation and Biology* 13:80–90.
- Rose, J. P., B. J. Halstead, G. D. Wylie, and M. L. Casazza. 2018b. Spatial and temporal variability in growth of giant gartersnakes: plasticity, precipitation, and prey. *Journal of Herpetology* 52:40–49.
- Rose, J. P., and B. D. Todd. 2017. Demographic effects of prolonged drought on a nascent introduction of a semi-aquatic snake. *Biological Invasions* 19:2885–2898.
- Rossman, D. A., N. B. Ford, and R. A. Seigel. 1996. The garter snakes: evolution and ecology. University of Oklahoma Press, Norman, Oklahoma, USA.
- Royle, J. A., R. B. Chandler, R. Sollman, and B. Gardner. 2014. Spatial capture-recapture. Academic Press, Waltham, Massachusetts, USA.
- Sandercock, B. K., S. R. Beissinger, S. H. Stoleson, R. R. Melland, and C. R. Hughes. 2000. Survival rates of a neotropical parrot: implications for latitudinal comparisons of avian demography. *Ecology* 81:1351–1370.
- Sauer, J. R., and N. A. Slade. 1987. Uinta ground squirrel demography: Is body mass a better categorical variable than age? *Ecology* 68:642–650.
- Schofield, M. R., and R. J. Barker. 2011. Full open population capture–recapture models with individual covariates. *Journal of Agricultural, Biological, and Environmental Statistics* 16:253–268.
- Seber, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- Shine, R. 1994. Sexual size dimorphism in snakes revisited. *Copeia* 1994:326–346.
- Sparkman, A. M., A. M. Bronikowski, J. G. Billings, D. Von Borstel, and S. J. Arnold. 2013. Avian predation and the evolution of life histories in the garter snake *Thamnophis elegans*. *American Midland Naturalist* 170:66–85.
- Stanford, K., and R. King. 2004. Growth, survival, and reproduction in a northern Illinois population of the plains gartersnake, *Thamnophis radix*. *Copeia* 2004:465–478.
- Steen, D. A. 2010. Snakes in the grass: Secretive natural histories defy both conventional and progressive statistics. *Herpetological Conservation and Biology* 5:183–188.
- Tenan, S., R. B. O'Hara, I. Hendriks, and G. Tavecchia. 2014. Bayesian model selection: the steepest mountain to climb. *Ecological Modelling* 283:62–69.
- Todd, B. D., and B. B. Rothermel. 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad (*Bufo terrestris*). *Biological Conservation* 133:178–185.
- U.S. Fish and Wildlife Service. 1993. Determination of threatened status for the Giant Garter Snake. *Federal Register* 58:54053–54066.
- Valcarcel, P. M. 2011. Giant gartersnake spatial ecology in agricultural and constructed wetlands. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Wallace, K., A. Leslie, and T. Coulson. 2013. Re-evaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model. *Journal of Animal Ecology* 82:155–165.
- Winne, C. T., J. D. Willson, K. M. Andrews, and R. N. Reed. 2006. Efficacy of marking snakes with disposable medical cautery units. *Herpetological Review* 37:52–54.

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