

Estimates of Survival Probability from Two Populations of Giant Gartersnakes in California's Great Central Valley

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The loss and modification of freshwater ecosystems has led to high rates of imperilment for freshwater species. The Giant Gartersnake (*Thamnophis gigas*) is among the species that have suffered declines in abundance and spatial distribution and is currently listed as a threatened species by the U.S. government and the State of California. Conservation and management of populations of *T. gigas* are hampered by a lack of information on its demography. Without estimates of demographic parameters, the status of the population is difficult to characterize, and identifying the parameters to target in management planning is problematic. We used capture–recapture data from two populations in the Great Central Valley of California to estimate annual survival probability. We also evaluated hypothesized causes of variation in survival probability among individuals and among years. Model-selection results for the population in the American Basin indicated that females have a higher survival probability than males and that survival probability and the amount of precipitation between 15 April and 15 May in a year are negatively correlated. Associations with other weather covariates were also supported, but the evidence was weaker. For the population in the Natomas Basin, the model-selection results indicated a positive association between survival probability and the body size of an individual (snout-to-vent length). There was also evidence that females have higher survival probabilities than males, but the support for this effect was weaker. This work fills gaps in our understanding of the demography of *T. gigas* by providing estimates of survival probability for males and age classes for which estimates were previously not available.

RIVERS, lakes, and wetlands in the United States have been heavily modified since the establishment of permanent human settlements by European immigrants (Benke, 1990). Estimates of the total area of wetlands in the contiguous U.S. indicate a decline greater than 50% from the mid-1700s to the mid-1900s, and losses in many states exceed 70% (Frayer et al., 1983; Dahl, 1990). Among the most dramatic examples of human-induced environmental change is the loss of expansive wetlands within California's Great Central Valley (hereafter Central Valley), which covers almost 110,000 km², about 40% of California's total area. Prior to the mid-1800s, approximately one third (53,000 km²) of the Central Valley was comprised of wetlands. However, as a result of incentives such as the Swamp Lands Act of 1850 (Peterson, 1974; Gates, 1975), an estimated 93% reduction in California's total wetlands has occurred through agricultural development, water diversion and damming, and urbanization (Frayer et al., 1989).

Due primarily to the considerable alterations of freshwater ecosystems, a large number of freshwater species are now imperiled (Allan and Flecker, 1993; Stein, 2001), and predicted extinction rates for freshwater fauna are higher than rates for terrestrial and coastal marine fauna (Ricciardi and Rasmussen, 1999). The high rates of decline in populations of freshwater species and relative lack of attention given to these taxa have led to calls for more urgent action (e.g., Allan and Flecker, 1993; Abell, 2002). Modification of hydrologic systems in the Central Valley has played an important role in declines and extinctions of aquatic invertebrates (Eng et al., 1990), fishes (Moyle, 1995),

and amphibians (Fisher and Shaffer, 1996). They have also led to declines in the abundance and spatial distribution of *Thamnophis gigas* (Giant Gartersnake) and, as a result, the species is listed as threatened by the U.S. government (USFWS, 1993) and the State of California (California Code of Regulations, 1971). *Thamnophis gigas* is endemic to California's Central Valley and is more closely associated with aquatic environments than other gartersnakes in California (Fitch, 1940). *Thamnophis gigas* uses low gradient streams, valley floor wetlands, and marshes and requires wetlands for foraging, upland areas for basking, upland burrows as summer shelter, and higher elevation uplands for winter hibernation (USFWS, 1993, 1999, 2012). In areas where wetlands have been reclaimed for agriculture, *T. gigas* is associated with rice agriculture and the water supply channels supporting its practice (USFWS, 1999).

One barrier to conservation of *T. gigas* is a lack of information on the demography of populations and the effects of environmental conditions on demographic rates. Unfortunately, although these factors are central to developing management plans for threatened or endangered species (Dodd, 1987, 1993), snakes are notoriously difficult to capture, and many authors have reported low capture probabilities from capture–recapture studies (e.g., Lind et al., 2005; Breininger et al., 2012; Hyslop et al., 2012). Secretive and wary behavior and cryptic coloration are common attributes of snakes, and many species use refugia when environmental conditions are poor and may be unavailable for capture during sampling. Although capture probability is rarely the parameter of primary interest, low capture

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probabilities generally result in poor precision in estimates of other demographic rates and in estimates of regression coefficients that link these rates to environmental covariates (Mazerolle et al., 2007). In spite of the challenges of sampling populations of *T. gigas*, some demographic rates have been estimated. Using capture–recapture data, Wylie et al. (2010) estimated density of *T. gigas* in four study areas in the Central Valley, and Halstead et al. (2012) estimated annual survival probability of adult female *T. gigas* using data from individuals with implanted radio transmitters. However, annual survival probability for males and other age or size classes of *T. gigas* have not previously been estimated, and information on other demographic parameters, including sex-specific growth and age structure and sex- and age-specific reproductive rates, is sparse. Our primary objective was to bolster knowledge of demography of *T. gigas* and thereby to inform management, by estimating annual survival probability for both males and females in two populations in the Central Valley. We also evaluated associations between survival probability and attributes of individuals (e.g., sex and size). Finally, a previous study noted high annual variation in survival probability of *T. gigas* (Halstead et al., 2012), and we hypothesized that weather was a likely cause. Therefore, we evaluated associations between survival probability and seasonal weather conditions.

MATERIALS AND METHODS

Study area.—We collected data from two populations of *T. gigas*, and we will refer to them as the American Basin and Natomas Basin populations. The American Basin is a low-lying drainage depression on the floor of the Sacramento Valley (northern Central Valley; Fig. 1). Situated northeast of the confluence of the American and Sacramento rivers, the American Basin extends northward toward the Bear River. It is bounded on the west by the Sacramento and Feather rivers, and the eastern boundaries are determined by elevational clines marked by shifting soil types and changing hydrology.

Historically flooded by runoff from the western slopes of the Sierra Nevada Range, the southern American Basin was modified by reclamation levees, pumps, and canals in 1914, converting a prevailing marsh and wetland landscape to agricultural production (USFWS, 1999). Rich, impermeable, alluvial clays deposited by historical floods slow drainage within the Basin and encourage the rice agriculture that has come to dominate land use in the area since the 1940s. Reclamation has also divided the lower and central American Basin into two distinct segments that are separated by the Natomas Cross Canal (Fig. 1). Although both segments of the American Basin are within known distance of individual movement for *T. gigas* (Valcarcel, 2011; Wylie and Amarello, unpubl. data), extensive radio-telemetry and mark–recapture studies have not documented individuals moving between them (Hansen, unpubl. data). Herein, we refer to the American Basin population as occurring in the predominantly rice-growing portion of the central or western American Basin that extends northward from the Natomas Cross Canal (Fig. 1). The Natomas Basin population occurs in the portion of the lower or southern American Basin that extends southward from the Natomas Cross Canal (Fig. 1) and consists of both agricultural wetlands and managed perennial wetlands.

Capture–recapture sampling.—We sampled populations of *T. gigas* in the American Basin from 2001 through 2012 and the Natomas Basin from 2004 through 2012. The resulting data reflect the longest continuous mark–recapture study of Giant Gartersnake populations in rice agriculture to date. We used visual encounter surveys and aquatic traps to capture snakes from approximately May through September (the sampling period) of each year. We set aquatic traps in all canals, ditches, and drains where water levels were sufficiently high to ensure that traps were continuously wetted, thereby reducing the risk of desiccation or thermal stress for captured snakes. We used galvanized 4-mesh eel pots (Tackle Factory [Cuba Specialty Manufacturing], Fillmore, New York), modified to float following the procedures in Casazza et al. (2000). We set clusters of 10–50 traps along each of 2–10 transects in each basin. In the Natomas Basin, we placed three transects in locations that did not change for the duration of the sampling period. We rotated each of the remaining seven transects among 35 locations at two-week intervals such that each location was trapped twice in each sampling period. In the American Basin, where emphasis was given to presence-absence and distribution sampling, we kept two transects in locations that did not change for the duration of the sampling period. We systematically relocated each of the remaining 0–11 transects (varying by year) after they had been in place a minimum of two weeks. We maintained and checked all traps daily while they were deployed.

We recorded the sex and measured the mass, total length, and snout-to-vent length (SVL) of each captured snake. We also classified snakes as infected with a parasitic nematode or not infected by inspecting their bodies for characteristic lesions or bumps. The nematode is from the genus *Eustrogyldes*, and its presence on *T. gigas* has been associated with impaired health, reduced growth rates, and mortality (USFWS, 1993, 1999). Passive integrated transponder (PIT) tags were implanted in captured snakes for permanent identification. In addition, we used medical cautery units to heat brand ventral scutes (i.e., microbranding; Winne et al., 2006) in a pattern consistent with scale-clip marking techniques (Brown and Parker, 1976) as a second mark for a subset of snakes. We also used microbranding to mark snakes too small (≤ 30 grams) to have PIT tags implanted. We released all snakes at the point of capture after processing and recording data.

Statistical analyses.—We structured the capture–recapture data for the Cormack–Jolly–Seber (CJS; Cormack, 1964; Jolly, 1965; Seber, 1965) data type by pooling data across all days of sampling in each year. Therefore, individuals were recorded as captured or not in each year. We fit models to the data in Program MARK (White and Burnham, 1999). Because the numbers of years of surveys differed between basins, we analyzed the data from American and Natomas basins separately. The two parameters in the CJS model are apparent survival probability (Φ_i) and recapture probability (p_i), where i indexes year. Apparent survival probability is the probability that an individual survives and remains in the sampled population from sampling in year i to sampling in year $i + 1$ (Lebreton et al., 1992). This parameter is referred to as apparent survival, because an individual that dies or permanently emigrates from the sampled population appears as a mortality. If an individual permanently emigrates and survives outside the sampled population,

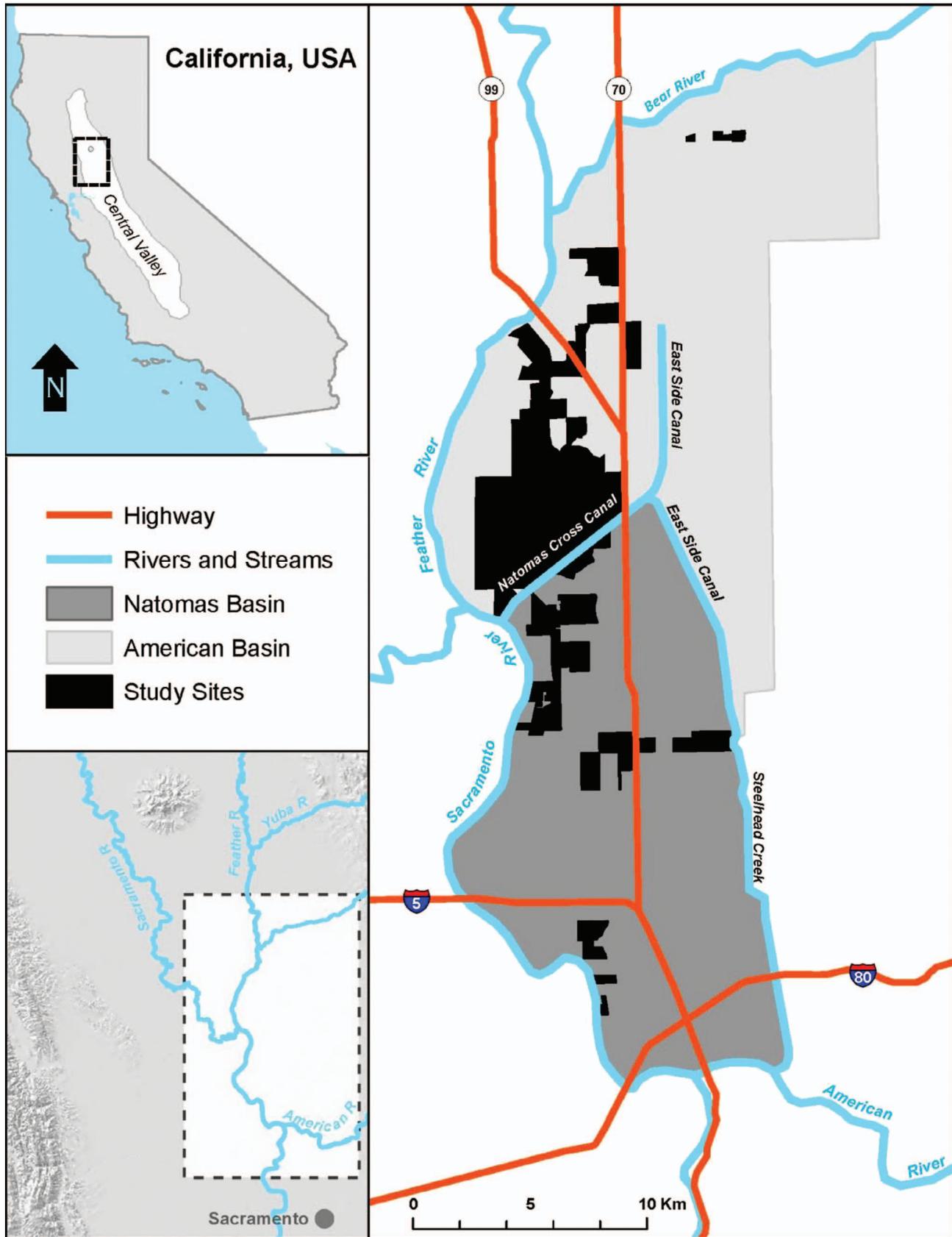


Fig. 1. Map of study area showing the location of the Central Valley within California (top left), the location of the study areas relative to Sacramento (bottom left), and a detailed map of the study basins (right). The American Basin (light gray) and Natomas Basin (dark gray) are separated by the Natomas Cross Canal. The locations of trapping within each basin are depicted in black.

Table 1. Weather covariates included in models of apparent survival probability of Giant Gartersnakes (*Thamnophis gigas*) in the American and Natomas basins of the Central Valley in California and their hypothesized association with apparent survival probability.

Season	Covariate	Abbreviation	Hypothesized association
Spring	Average daily minimum and maximum temperatures from 15 through 31 March	mar15.31.ave.min.temp, mar15.31.ave.max.temp	positive
Spring	Average daily minimum and maximum temperatures from 1 through 15 April	apr1.15.ave.min.temp, apr.1.15.ave.max.temp	positive
Spring	Sum of daily precipitation from 15 April through 15 May	apr15.may15.precip	negative or positive
Spring	The presence of a false spring, where 3 consecutive days of above- and below-average temperatures are required	false.spring.3	negative
Spring	The presence of a false spring, where 5 consecutive days of above- and below-average temperatures are required	false.spring.5	negative
Autumn	Average daily minimum or maximum temperatures from 15 September through 15 October	sep15.oct15.min.temp sep15.oct15.max.temp	positive

estimates of survival probability from the CJS model will be lower than true survival probability. The second parameter, recapture probability, p_i , is the probability that a marked individual is captured during sampling in year i .

Capture–recapture models are often composed of two or more types of parameters (e.g., survival and recapture probabilities in the CJS model), and different sets of hypotheses are often developed for each parameter. We refer to the mathematical representations of the hypotheses for each parameter as sub-models (*sensu* Taylor et al., 2005). We fit models to the data in three stages. First, we fit a set of 25 models that included combinations of sub-models of Φ_i and p_i with no variation (so-called “dot” models that are denoted as $\Phi [.]$ or $p[.]$), sex effects ($\Phi [s]$ or $p[s]$), year effects ($\Phi [t]$ or $p[t]$, where we treated year as a fixed effect) and additive or interactive effects of sex and year (Φ or $p[s + t]$ and $[s * t]$). We assessed the support in the data for each model on the basis of Akaike’s Information Criterion corrected for small sample size (AIC_c) and Akaike weights (w) (Hurvich and Tsai, 1989; Burnham and Anderson, 2002).

In the second stage of modeling, we used the model with the minimum AIC_c from the first stage to evaluate associations between recapture and apparent survival probability and four covariates: trap effort, marking method, presence of parasitic nematodes, and SVL. We hypothesized that recapture probability would vary temporally as a function of the number of trap nights associated with each study area and year (i.e., trap effort). We also hypothesized that apparent survival probability would be lower for individuals that were marked by a microbrand than for individuals in which we implanted a PIT tag. While the incision required to implant PIT tags is invasive, we sealed the wounds with surgical glue to keep the tags from falling out and to minimize the risk of infection. When we microbranded snakes, we inflicted three deep burns that were not sealed by surgical glue and released the snakes back into a septic environment. We used a time-varying individual covariate of the presence of nematodes to test the hypothesis that survival probability of individuals that are infected by the parasite is lower than that of uninfected individuals. We did not know if individuals were infected when they were not captured in a year and did not want to make assumptions about temporal dynamics of nematode infection in the snakes. Therefore, we only considered an individual infected in the first interval after nematodes were observed, which represents a conservative approach for testing the effect.

Finally, we hypothesized that apparent survival probability would increase as SVL increased and used year-specific measurements and estimates of SVL to test this hypothesis.

We interpolated or extrapolated values of SVL to obtain estimates for years when a snake was not captured and not measured. For all snakes that were recaptured in at least two years, we used the measurements of SVL across years to estimate growth rates. For the few snakes that were captured multiple times within a year, we used the first measurement of SVL. We fit three models of somatic growth to these data: the von Bertalanffy, logistic, and Richards. To fit each of the growth models, we assumed a difference equation, generally following White and Brisbin (1980). As an example, for the von Bertalanffy model:

$$L_{i+1} = (t_{i+1} - t_i)k(L_\infty - L_i) + L_i,$$

where L_i is the SVL in year i , t_i is the year of the observation, k is the von Bertalanffy growth coefficient, and L_∞ is the asymptotic SVL. To estimate SVL for years snakes were not captured, we applied the equation recursively, setting $t_{i+1} - t_i = 1$. For example, to estimate an SVL for 2010 from an SVL measured in 2006, we first applied the equation to the SVL measured in 2006 to estimate the SVL in 2007. We then used the estimate for 2007 to estimate the SVL for 2008, and so on until the 2010 length was estimated. We used this approach to produce values of SVL for each individual in each year after it was initially captured and selected among the von Bertalanffy, logistic, and Richards models on the basis of the smallest mean squared error.

In the third stage of modeling, we assessed the effect of weather on apparent survival probability by adding temperature and precipitation covariates to the model with the lowest AIC_c from the first stage. We identified spring (approximately mid-March to mid-April) and autumn (approximately mid-September to mid-October) as the most likely periods in which weather would influence survival probability. *Thamnophis gigas* is most active aboveground during these periods, and we suspect that its probability of survival is lower. In the spring, individuals are emerging from hibernacula and have been fasting for several months. We hypothesized that cool, wet weather in the spring will lower survival probability (Table 1) because lower temperatures and solar radiation could: 1) limit the ability of snakes to elevate body temperatures to levels needed for foraging and digestion and/or, 2) cause snakes to spend more time

thermoregulating by basking in the sun (heliothermic thermoregulation) or by adpressing their bodies to objects warmed by the sun (thigmothermic thermoregulation), which may increase their probabilities of predation and road mortality. These mechanisms may cause greater mortality in years with “false springs” than in years without them. We defined a false spring as a three- or five-day period of warm weather from 15 through 31 March followed by a three- or five-day period of cooler weather from 1 through 15 April. The warm period in March may cause snakes to leave hibernacula and commit to feeding and mating (EH, pers. obs.), which could expose them to unsuitable conditions during a period of cooler weather in April. In the autumn, survival probability of *T. gigas* may be lower in cooler years, especially if the rice harvest is early (Table 1). *Thamnophis gigas* migrates out of rice fields and other aquatic environments to terrestrial hibernacula in response to decreasing temperature and diminishing photoperiod in autumn (Wylie et al., 2009). If temperatures are relatively low during this period, *T. gigas* may spend more time thermoregulating, which increases the risk of predation and road mortality. In addition, if the harvest occurs before temperature and photoperiod initiate migration, many individuals may remain in rice fields, and mortality associated with agricultural activities during harvest may be high.

To identify false springs, we compiled data from the weather station at Sacramento Executive Airport (station name: SACRMNTO.C; <http://www.ipm.ucdavis.edu/>). We chose this weather station because it is the nearest weather station to the basins from which reliable data are available. We used weather station data obtained daily to calculate the average daily minimum and maximum temperatures from 15 through 31 March and from 1 through 15 April of each year and used these values as covariates in models (Table 1). We used both minimum and maximum temperatures because we did not have any *a priori* information suggesting either would be more strongly associated with Φ_i . We also computed the sum of daily precipitation from 15 April through 15 May. Higher precipitation over this period may reduce agricultural activity and associated mortality (a positive effect on survival probability), delay the harvest in fall and reduce harvest-related mortality in *T. gigas*, or make snakes more vulnerable to predation as they thermoregulate to maintain temperatures necessary for foraging (a negative effect on survival probability; Wylie et al., 2009).

We tested whether the presence of a false spring was associated with changes in survival probability in two ways. First, we tested whether survival probability was associated with the interaction between average daily maximum or minimum temperatures from 15 to 31 March and average daily maximum or minimum temperatures from 1 through 15 April (i.e., the effect of temperature in late spring depends on the temperature in the early spring). Second, we treated occurrence of a false spring as a binary covariate. To determine if a false spring occurred in a given year, we compared daily maximum temperature to the 60-year average daily maximum temperature from 1–15 March. If there were at least three consecutive days on which the maximum temperature exceeded the 60-year average for those days, we classified the year as one with a warm period in early spring. For years with a warm period in early spring, we then compared the maximum daily temperatures to the 60-year average maximum daily temperature from 1

through 15 April. We defined a cold period as three consecutive days on which the maximum temperatures were lower than the 60-year averages for those days. We classified all years with a warm period in early spring and a cold period in late spring as years with false springs. To account for the possibility that three consecutive days was insufficient to affect *T. gigas*, we used the same procedure as above but classified the occurrence of a false spring on the basis of five consecutive days of temperatures that are above and below average (Table 1). At the Natomas Basin, there were three years with false springs using the three-day criterion and two years using the five-day criterion. At the American Basin, there were six and three years with false springs using the three- and five-day criteria.

We used the weather station data to evaluate hypothesized associations between apparent survival probability of temperature in autumn as well as the timing of rice harvest. We calculated the average daily minimum and maximum temperatures from 15 September to 15 October of each year (Table 1). To test for an effect of harvest on apparent survival probability of *T. gigas*, we used precipitation from 15 April through 15 May in the previous spring as an indication of the timing of harvest. High precipitation during that period of time may delay planting, which may result in a later harvest (Table 1).

We standardized the values for each weather covariate and used Pearson product-moment correlation analysis in R (R Core Team, 2013) to evaluate correlations among covariates. We specified single-covariate models with each of the covariates. In addition, we specified additive models with a maximum of two covariates. We did not combine two covariates in a model if their correlation coefficient was >0.60 . For inference, we use and report model-averaged estimates of Φ_i and p_i , along with 95% confidence intervals (CIs).

RESULTS

We recorded a total of 755 captures of 639 individuals in the American Basin and 1,272 captures of 1,129 individuals in the Natomas Basin. The minimum and maximum SVLs measured in the American Basin were 181 mm and 1200 mm for females and 377 mm and 794 mm for males. In the Natomas Basin, the minimum and maximum SVLs were 181 mm and 1144 mm for females and 194 mm and 886 mm for males. The von Bertalanffy model provided the best fit of the three growth models based on the smallest mean squared error. Therefore, we used it to interpolate/extrapolate lengths. Parameter estimates from the von Bertalanffy growth model were $\hat{k}=0.27$ (SE = 0.02) and $\hat{L}_\infty=1021.20$ (SE = 25.00) for females and $\hat{k}=0.35$ (SE = 0.03) and $\hat{L}_\infty=738.40$ (SE = 13.70) for males.

The models from stages one and two with the lowest AIC_c values in the American Basin indicated that females have a higher apparent survival probability than males (Table 2). However, the AIC_c value for the model that includes sex was only 1 AIC_c unit lower than a model of no variation in Φ_i [i.e., $\Phi(\cdot), p(t)$], and the 95% CI for the estimated regression coefficient for the sex effect slightly overlapped zero. Model-averaged estimates of Φ_i for males in the American Basin ranged from 0.27 (0.11–0.52) to 0.53 (0.29–0.75) and from 0.34 (0.16–0.59) to 0.62 (0.37–0.82) for females. Although models that included the effects of microbranding, parasites, and SVL had AIC_c values similar to the highest-ranked model (Table 2), 95% confidence intervals on estimates of

Table 2. Model selection results for survivorship of Giant Gartersnakes (*Thamnophis gigas*) in the American Basin based on data from 2001–2012, for A) models that include individual covariates and trap effort (stage two) and B) models that include weather covariates (stage three). AIC_c = Akaike's Information Criterion adjusted for small sample size, ΔAIC_c = the difference between the AIC_c value for a model and the lowest AIC_c value, w_i = Akaike weight, k = the number of estimable parameters in the model, and $-2\log(L)$ = -2 times the log of the likelihood function at its maximum value. Abbreviations for covariates and effects other than weather are: s = sex, t = year effect, where year is treated categorically, Brand = presence of a microbrand, Parasite = presence of parasitic nematode, and SVL = snout-to-vent length.

	Model	AIC_c	ΔAIC_c	w_i	k	$-2\log(L)$
A	$\Phi(s), p(t)$	788.4	0.0	0.43	13	761.9
	$\Phi(s + \text{Brand}), p(t)$	789.6	1.2	0.24	14	761.0
	$\Phi(s + \text{Parasite}), p(t)$	790.3	1.9	0.17	14	761.7
	$\Phi(s + \text{SVL}), p(t)$	790.5	2.1	0.15	14	761.9
	$\Phi(s), p(\text{Trap Effort})$	797.4	9.0	0.01	4	789.4
B	$\Phi(s + \text{apr15.may15.prec} + \text{sep15.oct15.min.temp}), p(t)$	786.3	0.0	0.11	15	755.7
	$\Phi(s + \text{apr15.may15.prec}), p(t)$	786.6	0.3	0.09	14	758.0
	$\Phi(s + \text{apr15.may15.prec} + \text{sep15.oct15.max.temp}), p(t)$	787.0	0.7	0.08	15	756.4
	$\Phi(s + \text{apr1.15.max.temp}), p(t)$	787.3	1.0	0.07	14	758.7
	$\Phi(s + \text{apr15.may15.prec} + \text{mar15.31.min.temp}), p(t)$	787.4	1.1	0.06	15	756.7
	$\Phi(s + \text{apr15.may15.prec} + \text{mar15.31.max.temp}), p(t)$	787.6	1.3	0.06	15	756.9
	$\Phi(s + \text{apr15.may15.prec} * \text{sep15.oct15.min.temp}), p(t)$	788.0	1.7	0.05	16	755.3
	$\Phi(s + \text{apr1.15.max.temp} * \text{apr15.may15.precip}), p(t)$	788.1	1.8	0.05	16	757.4
	$\Phi(s), p(t)$	788.4	2.1	0.04	13	761.9

regression coefficients for those effects broadly overlapped zero and suggested no support for their importance.

The model selection results from the third stage at American Basin indicated a negative correlation between the amount of precipitation from 15 April through 15 May and apparent survival probability. The covariate for 15 April to 15 May precipitation was included in seven of the eight models with the lowest AIC_c values, and the 95% CI for the estimated regression coefficient for precipitation did not include zero. These models also suggested meaningful relationships between apparent survival probability and the average daily minimum and maximum temperatures from 15 September through 15 October (positive), average daily maximum temperature from 1 through 15 April (positive), and average daily minimum temperature from 15 through 31 March (positive), although the CIs for the estimates of regression coefficients for each covariate included 0.

With respect to recapture probabilities for *T. gigas* in the American Basin, the data most strongly supported a model of variation in recapture probability among years. Model-averaged estimates of recapture probabilities ranged from 0.08 (0.03–0.22) to 0.54 (0.32–0.74) and were <0.20 in five years.

The model with the lowest AIC_c value from the first stage of models of the data from the Natomas Basin included no effects on apparent survival probability and an effect of sex and year on recapture probability. The models with the second- and third-lowest AIC_c values ($\Delta AIC_c = 0.27$ and 1.48), however, included an effect of sex on apparent survival probability, and the estimate of the regression coefficient for sex from these models indicated higher survival probability for females, which is consistent with the results from the American Basin. Model-averaged estimates of recapture probability from the Natomas Basin ranged from 0.08 (0.04–0.15) to 0.26 (0.14–0.44) for females. Estimates were lower for males and ranged from 0.05 (0.02–0.10) to 0.18 (0.08–0.33).

Model selection results from the second and third stages indicated that, for *T. gigas* in the Natomas Basin, apparent

survival probability was positively associated with SVL (Table 3). The estimate of apparent survival probability from the highest ranked model for the smallest individual captured during the study (181 mm) was 0.37 (0.19–0.59), and the estimate for the largest individual (1144 mm) was 0.73 (0.54–0.87; Fig. 2). We found no support for effects of weather on apparent survival probability of *T. gigas* in the Natomas Basin for the period of study.

DISCUSSION

Information on the demography of threatened and endangered populations is an important component of management and conservation planning (Silvertown et al., 1996; Mills et al., 1999). Estimates of demographic rates for many species of plants and animals have been used to parameterize matrix models and identify the age- and sex-specific rates with the biggest effect on population growth (e.g., Doak et al., 1994 [Desert Tortoise, *Gopherus agassizii*]; Mayberry and Elle, 2010 [a perennial herb, *Actaea elata*]; and Johnson et al., 2010 [Sierra Nevada Bighorn Sheep, *Ovis canadensis sierrae*]). Inferences from these analyses allow managers to direct future research and conservation actions at the biotic and abiotic factors affecting those rates. The demography of *T. gigas* is poorly understood. The only demographic rate that has been estimated is the survival probability of large females (Halstead et al., 2012). Yet, studies of the demography of species of *Thamnophis* have reported differences in survival probability between sexes and size or age classes (Bronikowski and Arnold, 1999 [Western Terrestrial Gartersnake, *T. elegans*]; Stanford and King, 2004 [Plains Gartersnake, *T. radix*]; Lind et al., 2005 [Pacific Coast Aquatic Gartersnake, *T. atratus*]). In addition, the estimates from Halstead et al. (2012) are from snakes with surgically implanted radio-transmitters, an invasive procedure that may affect survival probability and bias inferences to the rest of the population. Estimates of demographic rates from males and other age classes and from different types of data

Table 3. Model selection results for survivorship of Giant Gartersnakes (*Thamnophis gigas*) in the Natomas Basin based on data from 2004–2012, for A) models that include individual covariates and trap effort (stage two) and B) models that include weather covariates (stage three). AIC_c = Akaike's Information Criterion adjusted for small sample size, ΔAIC_c = the difference between the AIC_c value for a model and the lowest AIC_c value, w_i = Akaike weight, k = the number of estimable parameters in the model, and $-2\log(L) = -2$ times the log of the likelihood function at its maximum value. Abbreviations for covariates and effects other than weather are: s = sex, t = year effect where year is treated categorically, Brand = presence of a microbrand, Parasite = presence of parasitic nematode, and SVL = snout-to-vent length.

	Model	AIC_c	ΔAIC_c	w_i	k	$-2\log(L)$
A	$\Phi(SVL), p(s + t)$	1086.0	0.0	0.53	11	1063.7
	$\Phi(\cdot), p(s + t)$	1087.4	1.4	0.26	10	1067.2
	$\Phi(\text{Brand}), p(s + t)$	1089.2	3.2	0.11	11	1067.0
	$\Phi(\text{Parasite}), p(s + t)$	1089.2	3.2	0.10	11	1067.0
	$\Phi(\cdot), p(s + \text{Trap Effort})$	1119.1	33.2	0.0	4	1111.1
B	$\Phi(SVL), p(s + t)$	1086.0	0.0	0.15	11	1063.7
	$\Phi(SVL + \text{sep15.oct15.min.temp}), p(s + t)$	1087.3	1.3	0.07	12	1063.1
	$\Phi(\cdot), p(s + t)$	1087.4	1.4	0.07	10	1067.2
	$\Phi(SVL + \text{mar15.31.min.temp}), p(s + t)$	1087.4	1.4	0.07	12	1063.2
	$\Phi(SVL + \text{apr15.may15.prec}), p(s + t)$	1087.6	1.6	0.06	12	1063.4
	$\Phi(SVL + \text{sep15.oct15.max.temp}), p(s + t)$	1087.7	1.7	0.06	12	1063.4
	$\Phi(SVL + \text{apr1.15.max.temp}), p(s + t)$	1087.9	1.9	0.06	12	1063.7
	$\Phi(SVL + \text{apr1.15.min.temp}), p(s + t)$	1087.9	1.9	0.05	12	1063.7
	$\Phi(SVL + \text{mar15.31.max.temp}), p(s + t)$	1087.9	1.9	0.05	12	1063.7

are needed to expand our understanding of the life history of *T. gigas* and validate previously published estimates.

The results of our analyses provide additional evidence of variation in survival probability among sexes and size or age classes of gartersnakes. The most strongly supported models of the data from the American Basin indicate higher survival probability for females than males, and the results from the Natomas Basin provided weaker support for the same pattern. Model-averaged estimates of survival probability from the American Basin are approximately ten percentage points higher for females than males (Fig. 2), which is similar to differences between the sexes in populations of *T. radix*

and *T. atratus* (Stanford and King, 2004; Lind et al., 2005). Among the largest snakes in the genus, *T. gigas* is a sexually dimorphic species. Females can reach sizes in excess of 1.6 m and 950 g, whereas males seldom exceed 250 g. Therefore, the differences in survival probability in the American Basin may be caused by variation in size between the sexes or variation in behavior between the sexes. However, we fit a model that included SVL to the data from the American Basin and found no evidence for higher survival in individuals with higher SVL. One possible behavioral cause for the difference is related to courtship and gestation. Males expend considerable energy in early spring searching for

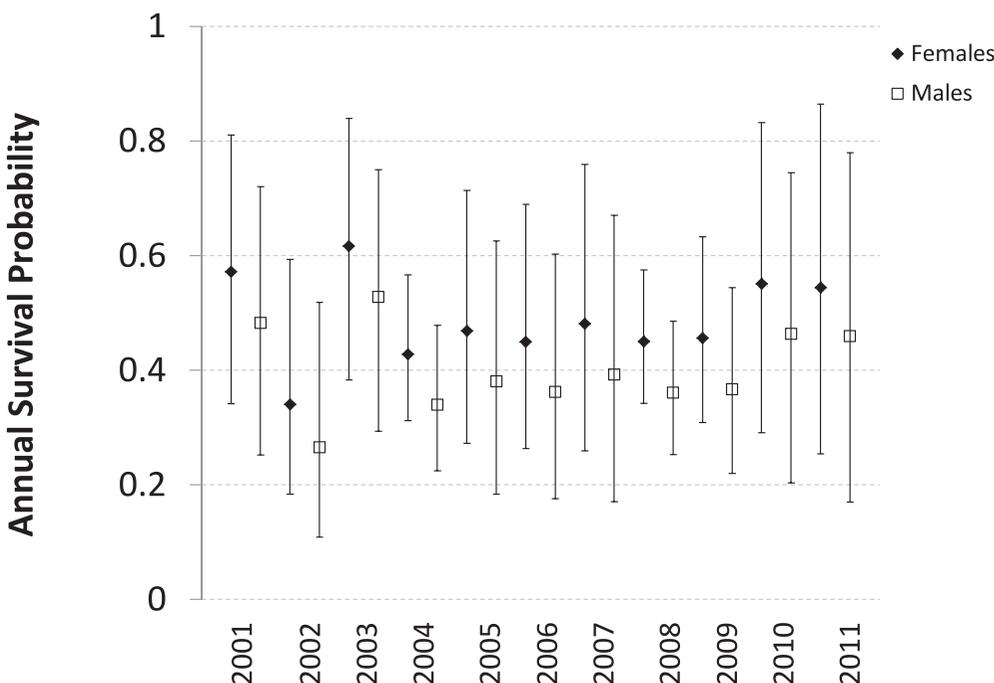


Fig. 2. Model-averaged estimates of annual survival probability (bars represent 95% confidence intervals) from capture–recapture data from male (solid black squares) and female (open triangles) Giant Gartersnakes (*Thamnophis gigas*). The sampled population is from the American Basin in the Central Valley of California.

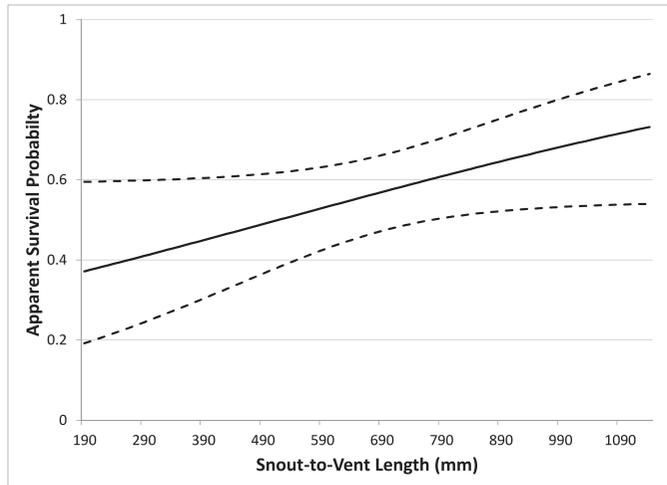


Fig. 3. Relationship between apparent survival probability and size (snout-to-vent length [SVL]) for Giant Gartersnakes (*Thamnophis gigas*) from the Natomas Basin. The solid black line represents point estimates from the highest ranked model, and the dashed black lines represent the lower (LCL) and upper (UCL) 95% confidence limits. The regression equation on the logit scale is: $\Phi = -0.833 + 0.002 \cdot SVL$.

mates. These movements occur shortly after they emerge from hibernacula and before they have had a chance to replenish depleted reserves of energy (Coates et al., 2009). Their body condition during this time of year is substantially lower than that of females (Coates et al., 2009), which may affect male survival probability.

In contrast to the results from the American Basin, the model selection results from the Natomas Basin provide support for an effect of SVL on survival probability (Table 3). Estimates of survival probability for larger *T. gigas* (~1100 mm) are approximately double the survival probability of the smallest individuals (~180 mm), although the estimates are imprecise and their 95% confidence intervals slightly overlap (Fig. 3). Stanford and King (2004) also reported differences in survival probability among age classes in a population of *T. radix*. Many species prey on *T. gigas* (USFWS, 1999; Carpenter, 2002), and a possible cause of the differences in survival probability between the size and age classes is differential predation pressure. The larger body size of females and adults may reduce the suite of species capable of capturing and killing individuals (Sparkman et al., 2013). We did not recapture snakes in every year and used the von Bertalanffy growth model to estimate SVL for individuals in years they were not captured. Although these values are estimates, we treated them as if they were known and did not account for uncertainty in the estimates in models. Therefore, estimates of standard errors for the regression coefficients are likely underestimated, and our inferences regarding an association between survival probability and SVL in the Natomas Basin population may be overstated.

We built on the work of Halstead et al. (2012), who reported high temporal variation in survival probability of *T. gigas*, by evaluating potential causes of the variation. We hypothesized that change in weather conditions across years was a likely cause of the variation either through direct mortality or through effects on the timing of agricultural activities. Evaluations of relationships between weather and the demography of snakes are uncommon

(Bronikowski and Arnold, 1999). Model selection results from the analysis of the data from the American Basin indicated a negative correlation between survival probability and the amount of precipitation from 15 April to 15 May. Examination of estimates of survival probability across years suggests that this relationship is largely caused by a year of relatively low survival from 2002 to 2003 when precipitation was more than 2 standard deviations higher than the mean over the 12 years of the study. The model selection results also suggested other relationships between weather covariates and survival probability of *T. gigas* in the American Basin, though the strength of the evidence for these relationships was weaker. Our analysis did not provide strong support for effects of weather on survival probability of snakes at the Natomas Basin. However, the capture–recapture data from the Natomas Basin are shorter in duration (9 years versus 12 years at the American Basin), and consequently, the power to detect associations with weather variables in the Natomas Basin was lower. In addition, aquatic habitats within the Natomas Basin include perennial wetland preserves managed to benefit *T. gigas*, providing a potential buffer from poor weather conditions and refuge from the mechanical threats associated with rice agriculture.

The previously published estimate of annual survival probability for large, radio-tagged females from Halstead et al. (2012) is 0.61 (95% credible interval: 0.41 to 0.79). However, this estimate represents an average among years, and, as we noted above, their results indicated considerable variation in survival probability among years (Halstead et al., 2012). Estimates of apparent survival probability for large females at the American Basin, for which there was no support for effects of sex or SVL, but strong support for annual variation, range from 0.34 (0.16 to 0.59) to 0.62 (0.37 to 0.82). The estimate for large females (1140 mm SVL) at the Natomas Basin, where there was only weak support for annual variation in apparent survival probability, is 0.73 (0.54–0.86). Generally, the confidence and credible intervals around these estimates broadly overlap, which indicates similar inferences from the two studies despite the fact that they used different field and analytical methods.

An assumption of the Cormack–Jolly–Seber model is that populations are sampled instantaneously (Lebreton et al., 1992; O’Brien et al., 2005). In practice, this assumption is addressed by keeping the sampling period short relative to the length of the interval between sampling periods. For species with physiological or behavioral traits that make them difficult to capture (e.g., many species of snakes [e.g., Lind et al., 2005; Breininger et al., 2012; Hyslop et al., 2012]), extending the length of the sampling period may be necessary to increase the probability of capturing individuals. If estimates of capture probability are too low, inference regarding estimates of demographic parameters and associations between those parameters and environmental covariates will have poor precision. Increasing the length of the sampling period, however, may cause bias in estimates of survival probability as it violates the assumption of instantaneous sampling (Hargrove and Borland, 1994; O’Brien et al., 2005). Previous studies have estimated the bias in estimates of survival probability when sampling periods are long and found it to be low, especially when capture probability is >0.20 and survival probability over the sampling period is >0.50 (Hargrove and Borland, 1994). To maximize estimates of capture probability, we sampled

T. gigas over five months each year (May–September). Without expanding the sampling period, the number of captures would not have been adequate. Even with the expanded sampling period, estimates of recapture probability for *T. gigas* in the American and Natomas basins were generally small (half of the estimates from the American Basin and all of the estimates from the Natomas Basin are < 0.3), and over 83% of the individuals in each basin were captured a single time. Consequently, the precision of estimates of survival probability is relatively low, as are the estimates of regression coefficients describing associations between survival probability and weather covariates. We initially attempted to fit more complex capture–recapture models (i.e., the Pradel [1996] model) to the data to estimate additional demographic rates (i.e., recruitment rates and population growth rates), but the imprecision of the estimates precluded meaningful inferences. Managers need reliable, precise estimates of demographic rates to guide decision-making processes and evaluate the effectiveness of their actions. Therefore, we suggest that improvements in field methods (e.g., Halstead et al., 2013) or evaluations of alternative sampling designs (e.g., the robust design [Pollock, 1982; Kendall et al., 1997]) become high priorities of future research. However, the need for more intensive sampling to attain adequate number of recaptures will need to be balanced with concerns about additional disturbance of an endangered species.

The estimates from this work, as well as the work of Halstead et al. (2012), have advanced our understanding of the demography of *T. gigas*, but important gaps in our knowledge remain. The estimates of survival probability suggest, on average, 30% to 40% of the population of neonates, juveniles, and adults dies each year. These individuals must be replaced by recruits into the population to prevent declines in abundance and extinctions of local populations. Yet, information on reproduction in *T. gigas* is sparse (Hansen and Hansen, 1990; Halstead et al., 2011). We are currently working with data from radiographed females to address questions regarding age at first reproduction, the relative contribution of various size classes of females to annual reproduction, and other aspects of the reproductive ecology of the species. A species' demographic patterns provide insight into its overall population dynamics and vulnerability to extinction, as species with slower rates of growth and reproduction are typically at higher risk and have longer recovery times after lean years or periods of decline (Shine and Schwartzkopf, 1992; Gotelli, 2001; Webb et al., 2002). Demographic models may also be used to compare populations at different sites, offering insight into which populations may be at greater risk and more in need of remedial management (Kunz, 1974; Schoener and Schoener, 1978; Gibbons et al., 1981). This information is essential as resource managers attempt to maintain populations of *T. gigas* in the Central Valley while contending with the myriad challenges associated with meeting California's complex water demands.

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