

Prepared in cooperation with the U.S. Fish and Wildlife Service

Distribution of Giant Gartersnakes (*Thamnophis gigas*) in the Sacramento–San Joaquin Delta, California, 2018–2019



Open-File Report 2020–1119

Cover Photo: Adult female giant gartersnake captured in the Sacramento–San Joaquin Delta, 2019.
Photograph taken by Kristen Fouts, U.S. Geological Survey.

Distribution of Giant Gartersnakes (*Thamnophis gigas*) in the Sacramento– San Joaquin Delta, California, 2018–2019

By Kristen J. Fouts, Richard Kim, Anna C. Jordan, Alexandria M. Fulton,
Jonathan P. Rose, Julia S. M. Ersan, and Brian J. Halstead

Prepared in cooperation with the U.S. Fish and Wildlife Service

Open-File Report 2020–1119

**U.S. Department of the Interior
U.S. Geological Survey**

U.S. Department of the Interior
DAVID BERNHARDT, Secretary

U.S. Geological Survey
James F. Reilly II, Director

U.S. Geological Survey, Reston, Virginia: 2020

For more information on the USGS—the Federal source for science about the Earth, its natural and living resources, natural hazards, and the environment—visit <https://www.usgs.gov> or call 1–888–ASK–USGS.

For an overview of USGS information products, including maps, imagery, and publications, visit <https://store.usgs.gov/>.

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Although this information product, for the most part, is in the public domain, it also may contain copyrighted materials as noted in the text. Permission to reproduce copyrighted items must be secured from the copyright owner.

Suggested citation:

Fouts, K.J., Kim, R., Jordan, A.C., Fulton, A.M., Rose, J.P., Ersan, J.S. M., and Halstead, B.J., 2020, Distribution of giant gartersnakes (*Thamnophis gigas*) in the Sacramento–San Joaquin Delta, California, 2018–2019: U.S. Geological Survey Open-File Report 2020–1119, 26 p., <https://doi.org/10.3133/ofr20201119>.

ISSN 2331-1258 (online)

Acknowledgments

We thank the numerous private landowners and agencies who provided access to their property to conduct giant gartersnake surveys. Without their cooperation, this study would not have been possible. M. Hayes, R. Klinger, and E. Nowak provided reviews of an earlier version of this report. We thank L. Parker for administrative assistance and many biological technicians, particularly A. Essert, D. Macias, D. Hammond, E. Schoenig, G. Napolitano, H. Hwang, J. Brown, J. Nagro, K. Miller, L. Kojima, L. Kong, L. Armistead, M. Guzman, M. Walters, M. Cook, P. Johnson, R. Elander, S. Malone, S. West, S. Williams, W. Erwin, and Z. Sheikh for their assistance with this project. We also thank K. Lopez and L. Meyers for their dedicated volunteer efforts. Snakes were handled in accordance with the University of California, Davis, Animal Care and Use Protocol WERC 2014-01 and as stipulated in the U.S. Fish and Wildlife Service Recovery Permit TE-157216-4.

Contents

Acknowledgments	iii
Introduction.....	1
Goals and Objectives.....	2
Methods.....	2
Field Methods	2
Analytical Methods.....	6
Results	7
Discussion.....	13
Summary.....	15
References Cited.....	15
Appendix 1 Supplemental Figures.....	18

Figures

1. Map showing initial proposed locations to sample for giant gartersnakes in the Sacramento–San Joaquin Delta, California, 2018–19.....	3
2. Map showing locations sampled for giant gartersnakes in the Sacramento–San Joaquin River Delta in summer 2018–19	4
3. Graphs showing the effects of year, salinity, prey availability, and emergent vegetation cover on probability of occurrence of giant gartersnakes in the Sacramento–San Joaquin Delta, California, 2018–19.....	8
4. Graph showing posterior distribution of the number of sampled sites occupied by giant gartersnakes in the Sacramento–San Joaquin Delta, California, 2018–19.....	9
5. Graph showing the effect of water temperature on giant gartersnake detection probability in the Sacramento–San Joaquin Delta, California, 2018–19.....	10
6. Graph showing median estimate of the number of consecutive non-detection surveys required to declare absence of giant gartersnakes in the Sacramento–San Joaquin Delta with 95-percent certainty based on prior probability of occurrence and water temperature	11

Tables

1. Summary of giant gartersnake captures and sampling effort at sites in the Sacramento–San Joaquin Delta, California, 2018–19.....	5
2. Prior and posterior distributions of parameters from the static occupancy model.....	6
3. Summary of all giant gartersnakes captured during summer 2018–19, including mass, snout-vent length, tail-vent length, and sex	7
4. Summary of giant gartersnake, valley gartersnake, mountain gartersnake, and Pacific gophersnake captures in the Sacramento–San Joaquin Delta during summer 2018–19.....	12

Conversion Factors

International System of Units to U.S. customary units

Multiply	By	To obtain
Length		
centimeter (cm)	0.3937	inch (in.)
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
Mass		
gram (g)	0.03527	ounce, avoirdupois (oz)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$^{\circ}\text{F} = (1.8 \times ^{\circ}\text{C}) + 32.$$

Abbreviation

SVL snout-vent length

Distribution of Giant Gartersnakes (*Thamnophis gigas*) in the Sacramento–San Joaquin Delta, California, 2018–2019

By Kristen J. Fouts, Richard Kim, Anna C. Jordan, Alexandria M. Fulton, Jonathan P. Rose, Julia S. M. Ersan, and Brian J. Halstead

Introduction

Of the many estuaries in North America, the Sacramento–San Joaquin River Delta (hereinafter the “Delta”) in Northern California is one of the largest. The Delta is an important ecosystem historically composed of expansive tidal marshes in which many species of wildlife thrived. In the last century, most of the marshes were transformed into agricultural land on the islands within the Delta by the construction of over 1,000 miles of levees. Remaining historical marsh is now composed of margins of tidal canals and areas within some Delta islands. In addition to agriculture, the Delta is important because it supplies most of California’s water for human uses. Because of these intensive uses, the Delta faces many ecological threats. Efforts are underway to restore parts of the ecosystem that have been affected while maintaining a viable water supply. These restoration efforts are intended to benefit a variety of unique fish and wildlife species including giant gartersnakes (*Thamnophis gigas*).

Giant gartersnakes comprise a large, wetland-obligate snake species endemic to California’s Great Central Valley. Giant gartersnakes exhibit sexual size dimorphism, with females in the Sacramento Valley achieving an average asymptotic length of median =910 (95-percent credible interval =865–954) millimeters (mm) snout-vent length (SVL) and males achieving an average asymptotic length of 690 (650–730) mm (Rose and others, 2018b). The snakes historically inhabited freshwater marshes and sloughs, but with the conversion of wetlands to agriculture in the Central Valley, most extant populations are now associated with rice agriculture in the Sacramento Valley (Halstead and others, 2010, 2019). During the active season, giant gartersnakes select emergent and terrestrial vegetation that provides cover, with a particularly strong affinity for hardstem bulrushes (*Schoenoplectus acutus*; also called “tules”; Halstead and others, 2016). Although giant gartersnakes use burrows near water throughout the year, subterranean features like burrows, cracks, and voids in rock or concrete, particularly those near marshes and canals but above the flood zone, are important for giant gartersnake hibernation (Halstead and others, 2015b). Giant gartersnakes primarily prey on frogs, fish, and tadpoles, and select native frogs over other potential

prey types (Ersan and others, 2020a, 2020b). In turn, otters, raptors, wading birds, large predatory fishes, and introduced American bullfrogs (*Lithobates catesbeianus*) prey on giant gartersnakes (Hansen, 1986; Wylie and others, 2003; Halstead and others, 2015c).

Much has been learned about giant gartersnake population ecology in the past decade. Giant gartersnakes produce a mean of 15.9 (± 4.6 standard deviation [SD], range =5–33) offspring per litter, with litter size positively related to the size of the female (Rose and others, 2018a). In the drought years 2014–16, only half to two-thirds of female snakes large enough to reproduce did so each year (Rose and others, 2018a). Giant gartersnake annual survival averages =0.45 (95-percent credible interval =0.30–0.61) and increases with size to near 0.51 for snakes approximately 800-mm SVL, after which survival either plateaus or decreases (Rose and others, 2018c). Survival also varies among sites and years, with increases in precipitation the previous year and vegetative cover positively affecting survival (Rose and others, 2018c). In some locations, survival also has been found to vary with snake sex, springtime precipitation, and minimum temperatures in the autumn (Hansen and others, 2015). Population growth of giant gartersnakes is most sensitive to survival of large females but depending on assumptions about the shape of the size-survival relationship, growth of juveniles also can have a relatively strong influence on population growth rate (Rose and others, 2019). Giant gartersnakes exhibit relatively low genetic diversity, with small effective population sizes and low genetic diversity in most populations (Wood and others, 2015). The population genetic structure of giant gartersnakes is closely linked with large drainage basins in the Central Valley, with some admixture of populations in the Delta (Wood and others, 2015).

Because of the loss of most marshes in the Central Valley, giant gartersnakes are listed under the Federal and State Endangered Species Act as threatened (California Department of Fish and Game Commission, 1971; U.S. Fish and Wildlife Service, 1993). Although they are now extirpated from most of the southern part of their former range, giant gartersnakes persist in the Sacramento Valley in remnant marshes and sloughs and rice-growing agricultural habitats (Halstead and others, 2010, 2014, 2015a; Hansen and others, 2017).

The distribution of giant gartersnakes in the Sacramento–San Joaquin Delta is mostly unknown but reports of giant gartersnake observations in the Delta have increased in recent years. Understanding the distribution of giant gartersnakes in the Delta is essential for conserving these snakes in this unique ecosystem.

Goals and Objectives

With the financial support of the U.S. Fish and Wildlife Service (USFWS), the primary objective of this project was to examine the distribution of giant gartersnakes in the Sacramento–San Joaquin Delta and to quantify landscape-level habitat, local microhabitat, vegetation composition, and prey count variables associated with the occurrence of giant gartersnakes. This study is an important early step for conservation planning for giant gartersnakes in the Delta. In particular, the results present findings on where giant gartersnakes occur and are likely to occur, which provides information for managing existing wetlands and prioritizing locations for wetland restoration for the benefit of giant gartersnakes and other species.

Methods

We used occupancy methods to evaluate the distribution of giant gartersnakes in the Sacramento–San Joaquin Delta. In this section, we provide a detailed description of the field and analytical methods.

Field Methods

The intended area of inference of this study was the Sacramento–San Joaquin Delta from Yolano in the north to California Route 4 in the south, and from Interstate Highway 5 in the east to Sherman Island in the west. Within this region, the USFWS identified priority islands and properties for sampling, including Bouldin Island, Bradford Island, Empire Tract, Jersey Island, King Island, Liberty Island, Lower Yolo Ranch, Mandeville Island, Sherman Island, Twitchell Island, Venice Island, Webb Tract, Woodward Island, and Yolano (fig. 1). Surveys were done in 2018 and 2019. We used a Generalized Random Tessellation Stratified design (Stevens and Olsen, 2004) implemented in the R package ‘spsurvey’ (Kincaid and Olsen, 2016) to randomly select 32 sites (wetlands, lakes, ponds, and canal reaches) in the priority

areas and 30 sites within the study region but outside the priority areas. We used the same procedures to select the same number of additional sites as an oversample to use in case we could not access the original 62 selected sites.

Following site selection, we attempted to identify and contact landowners for permission to sample using several tools. We first attempted to use the software ParcelQuest (Folsom, California, USA), which is essentially an electronic plat map. We also attempted to scout for sites and identify landowners based on signage near selected locations. Finally, we used word of mouth from contacts we identified to locate additional landowners on whose property we could sample. Once landowners were identified, we contacted them by phone, e-mail, or both, depending on the information we were able to obtain.

We completed sampling at the randomly selected sites in 2018, but limitations to site access caused by difficulties in identifying and contacting landowners and obtaining landowner permission forced us to abandon random sampling in 2019. Instead, we sampled opportunistically where access and permission were granted. In cases where USFWS interest warranted it, we resampled sites in 2019 that had been sampled in 2018 (fig. 2). The non-random sampling scheme that resulted from lack of access had important implications for inference from this study. For example, because sampled sites were ultimately determined by where permission was granted, the relationships between environmental variables and giant gartersnake occurrence apply only to the sample of sites and not to the Delta as a whole. Estimates of the probability of occurrence also apply only to the sampled sites, rather than as an estimate of the proportion of the Delta occupied by giant gartersnakes. We therefore stress that our study is primarily useful for finite-sample inference, rather than inference to the above-defined area of study (that is, inference about the actual sites sampled rather than the Delta; Link and Barker, 2010).

We placed transects based on landowner permission and field observations of habitat to maximize the likelihood of detecting giant gartersnakes. Where possible, we deployed a transect of 50 modified aquatic funnel traps spaced 10–20 meters (m) apart (Halstead and others, 2013) at each site. Transects ranged in length from approximately 500 m to 1 kilometer (km). We positioned transects along the banks of canals or at the edge of emergent vegetation in wetlands because giant gartersnakes forage along habitat edges, which act as natural drift fences that direct snake movement to traps. We deployed traps for 21 consecutive days and checked traps daily while they were deployed (table 1). We adjusted traps as necessary to maintain their effectiveness and prevent drowning or overheating of snakes.

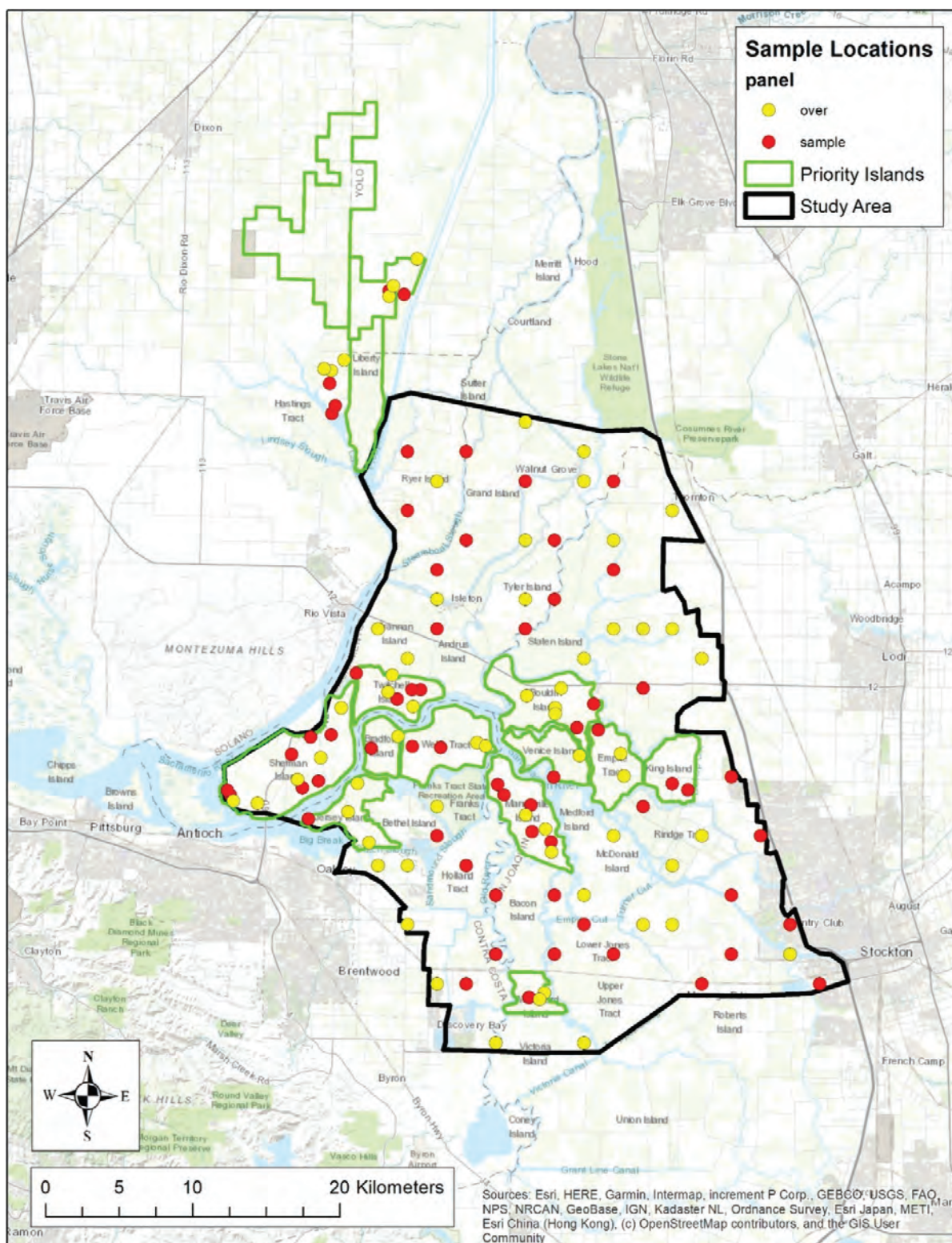


Figure 1. Initial proposed locations to sample for giant gartersnakes (*Thamnophis gigas*) in the Sacramento–San Joaquin Delta, California, 2018–19. “Panel” refers to whether the location was a site selected to be sampled (sample) or an oversample site to replace inaccessible sample sites (over).

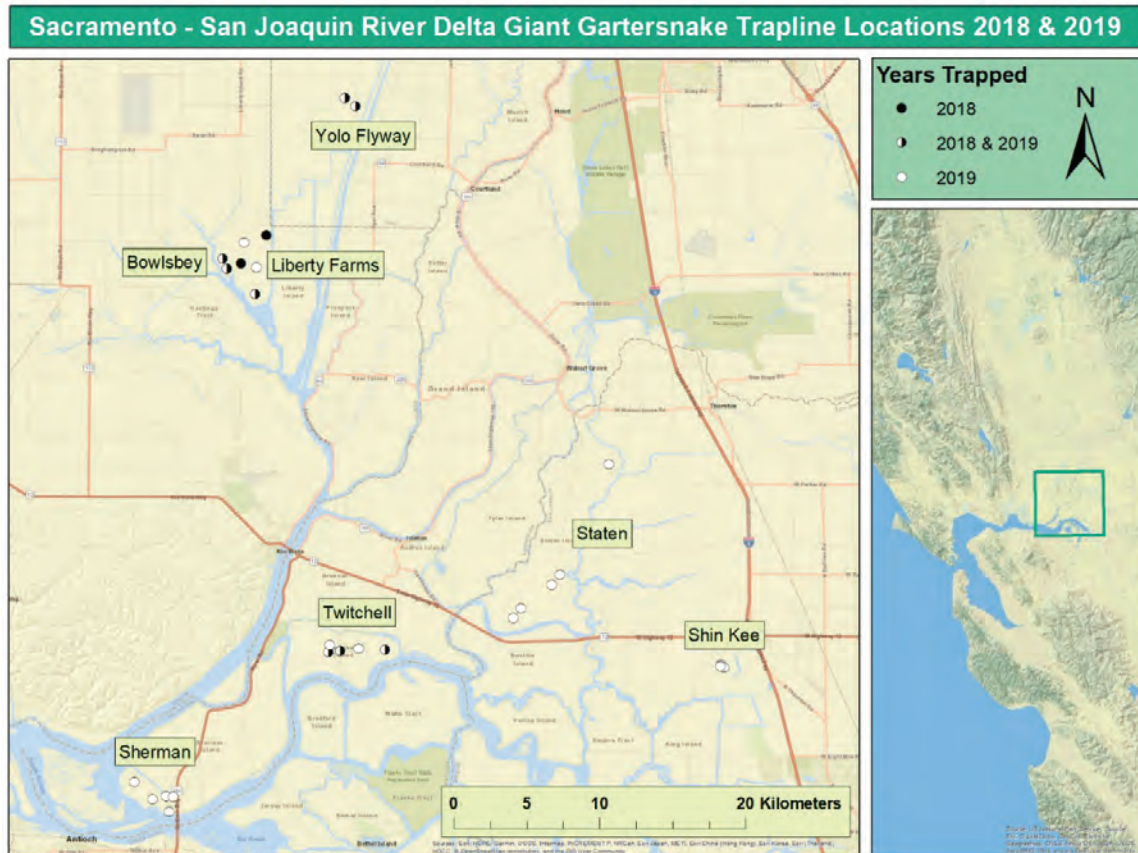


Figure 2. Locations sampled for giant gartersnakes (*Thamnophis gigas*) in the Sacramento–San Joaquin River Delta in summer 2018–19.

We monitored environmental conditions presumed to be related to giant gartersnake behavior at each transect. In particular, we measured daily water temperatures, air temperatures, and fluctuations in water level. We also recorded the contents of every fifth trap daily and then removed all contents from these traps to obtain a measure of the relative counts and diversity of prey species. All other traps were checked, but prey were allowed to remain in the traps so that they became naturally baited over time. We also recorded the number of active traps on each transect daily to account for differences in sampling effort caused by fluctuating water levels, trap damage, or trap theft. Large fluctuations in water level (areas of tidal influence or draining of wetlands or canals and ditches) at times necessitated abandonment of transects or relocation of transects to a suitable nearby location within the selected site. We measured salinity one time at the location of the water level stake at the establishment of the transect.

We recorded the Universal Transverse Mercator coordinates of all trap locations and completed vegetation and habitat surveys at points along and adjacent to each transect. We visually estimated the percent cover of habitat types (water, submerged vegetation, floating vegetation, emergent vegetation, terrestrial vegetation, rock, or bare ground) and vegetative composition (species or lowest discernible taxonomic category, in some cases divided by growth habit, such as single-stemmed, clumped, or turf-forming grasses) within a 1-m radius of every fifth trap. At each of the traps sampled for microhabitat and vegetation composition, we randomly selected a point to the left (odd-numbered traps) or right (even-numbered traps) of the transect (as viewed in ascending trap number) at a randomly selected perpendicular distance of 2–5 m where we then visually estimated percent cover of habitats and vegetative composition within a 1-m radius circle to better characterize habitat surrounding the traps.

Table 1. Summary of giant gartersnake (*Thamnophis gigas*) captures and sampling effort at sites in the Sacramento–San Joaquin Delta, California, 2018–19.

[Posterior probability of occurrence is based on site (salinity, emergent vegetation, and prey relative abundance) and survey (water temperature) characteristics and their estimated effects. Sites at which giant gartersnakes were detected had a posterior probability of 1.000. Prior probability of occurrence across sites was uninformative ($\text{beta}[1, 1]$ distribution, which is uniform from 0 to 1). **Abbreviation:** —, site was not sampled that year]

Site	Number of giant gartersnakes captured		Dates trapped		Total trap-days		Posterior probability of occurrence	
	2018	2019	2018	2019	2018	2019	2018	2019
Bowlsbey 1	0	0	Jul 24–Aug 14	Jul 9–Jul 30	1,048	1,050	0.401	0.489
Bowlsbey 2	0	1	Jul 24–Aug 14	Jul 9–Jul 30	1,049	1,050	0.619	1.000
Liberty Farms 1	7	0	Jun 27–Jul 21	Jul 10–Jul 31	1,100	1,044	1.000	0.312
Liberty Farms 2	0	—	Jul 14–Aug 4	—	1,048	—	0.460	—
Liberty Farms 3	0	—	Jul 20–Aug 13	—	1,199	—	0.367	—
Liberty Farms 4	—	1	—	Jul 27–Aug 17	—	1,050	—	1.000
Liberty Farms 5	—	1	—	Jul 30–Aug 20	—	1,049	—	1.000
Sherman 1	—	0	—	Aug 26–Sep 18	—	1,049	—	0.260
Sherman 2	—	0	—	Aug 27–Sep 19	—	1,049	—	0.149
Sherman 3	—	0	—	Aug 28–Sep 20	—	1,049	—	0.141
Sherman 4	—	0	—	Aug 29–Sep 21	—	1,049	—	0.588
Sherman 5	—	1	—	Aug 29–Sep 22	—	1,100	—	1.000
Shin Kee 1	—	1	—	Sep 7–Sep 28	—	1,050	—	1.000
Shin Kee 2	—	1	—	Sep 8–Sep 29	—	1,048	—	1.000
Shin Kee 3	—	0	—	Sep 10–Oct 1	—	1,050	—	0.311
Staten 1	—	0	—	Aug 6–Aug 27	—	1,046	—	0.216
Staten 2	—	0	—	Aug 7–Aug 28	—	1,050	—	0.421
Staten 3	—	0	—	Aug 7–Aug 28	—	1,049	—	0.109
Staten 4	—	0	—	Aug 13–Sep 5	—	1,050	—	0.128
Staten 5	—	0	—	Aug 19–Sep 11	—	1,021	—	0.240
Twitchell 1	0	0	Aug 31–Sep 16	Aug 16–Sep 8	700	1,046	0.140	0.169
Twitchell 2	0	0	Aug 31–Sep 23	Aug 21–Sep 13	1,049	1,047	0.711	0.263
Twitchell 3	0	0	Sep 1–Sep 24	Aug 17–Sep 9	1,050	1,050	0.647	0.579
Twitchell 4	—	0	—	Aug 22–Sep 14	—	1,049	—	0.751
Twitchell 5	—	0	—	Aug 23–Sep 15	—	1,041	—	0.181
Yolo Flyway 1	1	0	Jun 26–Jul 19	Jul 31–Aug 21	1,093	1,050	1.000	0.300
Yolo Flyway 2	0	0	Jun 27–Jul 20	Jul 30–Aug 21	1,042	1,050	0.258	0.322
Total	8	6	Jun 26–Sep 24	July 9–Oct 1	10,378	26,236	0.49 (0.07–0.95)	0.18 (0.02–0.81)

We used scale measurements (Rossman and others, 1996) to verify the species of each captured gartersnake. We measured snout-vent length and tail length of each individual to the nearest 1.0 mm and weighed each individual to the nearest 1.0 gram (g). We determined the sex of the individuals by probing the cloaca to detect the presence or absence of hemipenes. After examination, each individual was given a unique brand on its ventral scales (Winne and others, 2006) and if large enough (greater than 30 g), the individual was

implanted with a passive integrated transponder (PIT) tag injected subcutaneously at scale row three approximately 5 centimeters (cm) anterior to the vent. The injection site was sealed with cyanoacrylate glue to prevent the PIT tag from migrating out through the opening in the skin prior to it healing. Each individual was released at its location of capture immediately after processing.

Analytical Methods

We evaluated the probability of occurrence (occupancy, ψ) of giant gartersnakes in 2018 and 2019 using single-season (static) occupancy models (Kéry, 2010; MacKenzie and others, 2002, 2006; Thompson and others, 2004). We used static, rather than dynamic, occupancy models because data were of too short a duration and too sparse to estimate colonization and extirpation probabilities. Instead, we accounted for potential differences in probability of occurrence across years by counting each site by year combination as an independent site for analysis but included a fixed effect of year on the probability of occurrence. We estimated effects of salinity, percent cover of emergent vegetation, and prey availability (sum of the detections of fish, tadpoles, and frogs captured per trap) on probability of giant gartersnake occurrence at each trapline as constant across years to increase statistical power to detect the effects of these covariates. Because of the limited number of giant gartersnake captures, and because we used the same number of the same type of traps across years, we excluded the year effect for detection probability but included an effect of water temperature, which consistently affects detection probabilities of giant gartersnakes in the Sacramento Valley (Halstead and others, 2011).

We analyzed the models using Bayesian inference by Markov-chain Monte Carlo methods (Royle and Dorazio, 2008; Kéry, 2010; Link and Barker, 2010). Posterior inference was based on three chains of 33,333 iterations each, after a burn-in period of 10,000 iterations, resulting in 999,999 iterations to describe the posterior distribution of each parameter. We used uninformative priors (prior distributions that assume no prior information about the effects of the variable on the response exists; table 2) because our previous giant gartersnake sampling data was from rice-growing regions of the Sacramento Valley and it was unlikely these data were appropriate in the Delta. We standardized (in other words, z -transformed) all continuous covariates to have a mean =0 and standard deviation (SD) =1 by subtracting the sample mean from the observed value (centering) and dividing by the sample standard deviation to improve interpretability of model coefficients. We assessed model goodness-of-fit with a Bayesian P -value (Kéry and Royle, 2016). We also derived the number of occupied sampled sites each year, the posterior probability each site was occupied, and the number of consecutive non-detection surveys under average survey conditions required to infer giant gartersnake absence with 95-percent certainty (Wintle and others, 2012).

Table 2. Prior and posterior distributions of parameters from the static occupancy model.

[Posterior distributions are presented as median (95-percent symmetrical credible interval). Odds ratios describe the change in odds of occupancy or detection with a one standard deviation increase in the variable (2.7 degrees Celsius water temperature, 0.8 ppt salinity, 20-percent cover of emergent vegetation, and 2.0 prey/[trap-day]) and are presented for coefficients only. **Abbreviation:** —, not applicable]

Parameter description	Symbol	Prior distribution	Posterior distribution	Posterior probability of effect in direction of median	Odds ratio
Mean detection probability (p)	μ_p	$beta(\alpha = 1, \beta = 1)$	0.03 (0.01–0.07)	—	—
Effect of water temperature on p	α_{temp}	$Gaussian(\mu = 0, SD = 2)$	0.48 (–0.12–1.08)	0.94	1.62 (0.88–2.96)
Mean probability of occurrence (ψ) in 2018	μ_ψ	$beta(1, 1)$	0.49 (0.07–0.95)	—	—
Effect of year 2019 on ψ	β_{2019}	$Gaussian(0, 2)$	–0.34 (–3.01–2.74)	0.60	0.71 (0.05–15)
Effect of salinity on ψ	$\beta_{salinity}$	$Gaussian(0, 2)$	–1.86 (–4.95–2.27)	0.88	0.16 (0.01–9.7)
Effect of emergent vegetation on ψ	β_{em_veg}	$Gaussian(0, 2)$	1.21 (–0.71–3.40)	0.91	3.3 (0.49–30)
Effect of prey relative abundance on ψ	β_{prey}	$Gaussian(0, 2)$	–1.22 (–4.24–1.62)	0.84	0.29 (0.01–5.0)
Number of occupied sampled sites in 2018	—	—	6 (2–9)	—	—
Number of occupied sampled sites in 2019	—	—	11 (6–22)	—	—

We analyzed each model with JAGS software, version 4.3.0 (Plummer, 2017) called from R version 3.6.1 (R Core Team, 2019) using the package ‘jagsUI’ (Kellner, 2018). We diagnosed convergence with visual examination of history plots and with the Gelman-Rubin statistic (Gelman and Rubin, 1992); no evidence for lack of convergence was observed. The minimum effective sample size for any monitored parameter was 2,253. We summarize posterior distributions as median (95-percent symmetrical credible interval) unless otherwise indicated. Odds ratios describe the change in odds of occupancy or detection with a one standard deviation increase in the variable (2.7-degrees Celsius [$^{\circ}\text{C}$] water temperature, 0.8-parts per thousand (ppt) salinity, 20-percent cover of emergent vegetation, and 2.0 prey/[trap-day]) and are presented for coefficients only.

Results

Overall, we detected giant gartersnakes at 8 of 27 sampled trap transects on 3 of 6 sampled islands (table 1). In 2018, we captured 8 giant gartersnakes at 2 of the 10 trap transects (1 capture of 1 snake at Yolo Flyway 1; 8 captures of 7 snakes at Liberty Farms 1) over 10,378 trap-days. In 2019, we captured 6 giant gartersnakes once each at 6 of the 25 trap transects over 26,236 trap-days (table 1). Of the eight sites that were sampled in both 2018 and 2019, two trap transects changed detection status between years: snakes were detected at Liberty Farms 1 in 2018 but not 2019, and snakes were not detected at Bowlsbey 2 in 2018 but were detected in 2019 (table 1). Specific locations sampled and locations of giant gartersnake captures in 2018 and 2019 are found in appendix 1. Three females and four males were captured in 2018, and four females and two males were captured in 2019 (table 3). Of the giant gartersnakes captured in 2018, two females were adults and one was likely approximately 1-year old (born in 2017) based on their mass and SVL. The four males captured were adults. Of the giant gartersnakes captured in 2019, all four females and one male were adults, and the other male was approximately 1-year old (born in 2018) based on their mass and SVL (table 3).

The static occupancy model fit the data well (Bayesian P -value = 0.570), but none of the covariates were strong predictors of occurrence. The posterior distributions for the logit effect of year 2019 was neutral, salinity and prey availability were mostly negative, and emergent vegetation was mostly positive (table 2; fig. 3). Mean probability of occurrence in 2018 at a site with average covariate values was 0.49 (0.07–0.95), and in 2019 mean probability of occurrence was 0.18 (0.02–0.81; fig. 3). Of 10 sampled sites, 6 (2–9) sites were estimated to be occupied in 2018, whereas 11 (6–22) of 25 sampled sites were estimated to be occupied in 2019 (fig. 4). For every 0.8 ppt increase in salinity, giant gartersnakes were 0.16 (0.01–9.68) times as likely to occur at a trapline (fig. 3). For every 2.0 prey/(trap-day) increase

in prey relative abundance, giant gartersnakes were 0.29 (0.01–5.03) times as likely to occur at a trapline (fig. 3). Giant gartersnakes were 3.35 (0.49–30.0) times more likely to occur at a trapline with a 20-percent increase in absolute cover of emergent vegetation (fig. 3).

Mean daily detection probability at an average water temperature of 22.3 $^{\circ}\text{C}$ was 0.03 (0.01–0.07). Water temperature had a positive effect on detection probability: for every 2.7 $^{\circ}\text{C}$ increase in water temperature, giant gartersnake detection probability increased 1.62 (0.88–2.96) times (probability positive = 0.942; fig. 5). Over the course of a 21-day trap deployment, the cumulative probability of detecting giant gartersnakes at a constant 22.3 $^{\circ}\text{C}$, given they occur at a trapline, was 0.48 (0.24–0.77). Given this detection probability, inferring absence with 95-percent certainty at a site with a prior probability of 0.5 of being occupied by giant gartersnakes would require 96 (43–231) consecutive days of non-detections (fig. 6).

In addition to giant gartersnakes, we also captured valley gartersnakes (*Thamnophis sirtalis fitchi*), mountain gartersnakes (*Thamnophis elegans elegans*), and Pacific gophersnakes (*Pituophis catenifer catenifer*) in our traps (table 4). In 2018, 34 captures of valley gartersnakes were made at 5 traplines. In 2019, 35 valley gartersnakes were captured at 11 traplines; 2 mountain gartersnakes were captured at 1 trapline, and 2 Pacific gophersnakes were captured at 2 traplines (table 4).

Table 3. Summary of all giant gartersnakes captured during summer 2018–19, including mass, snout-vent length, tail-vent length, and sex.

[g, gram; SVL, snout-vent length; mm, millimeter; TVL, tail-vent length]

Microbrand	Trapline	Mass (g)	SVL (mm)	TVL (mm)	Sex
2018					
12001	Liberty Farms 1	151	583	181	Male
12002	Liberty Farms 1	184	645	145	Male
12003	Yolo Flyway 1	29	405	116	Female
12004	Liberty Farms 1	97	602	121	Male
12005	Liberty Farms 1	129	620	176	Male
12006	Liberty Farms 1	535	985	170	Female
12007	Liberty Farms 1	255	757	191	Female
2019					
12008	Bowlsbey 2	251	791	140	Female
12009	Liberty Farms 5	200	703	213	Male
12010	Liberty Farms 4	177	710	50	Female
12011	Sherman 5	50	499	153	Male
12012	Shin Kee 2	201	710	191	Female
12013	Shin Kee 1	259	762	86	Female

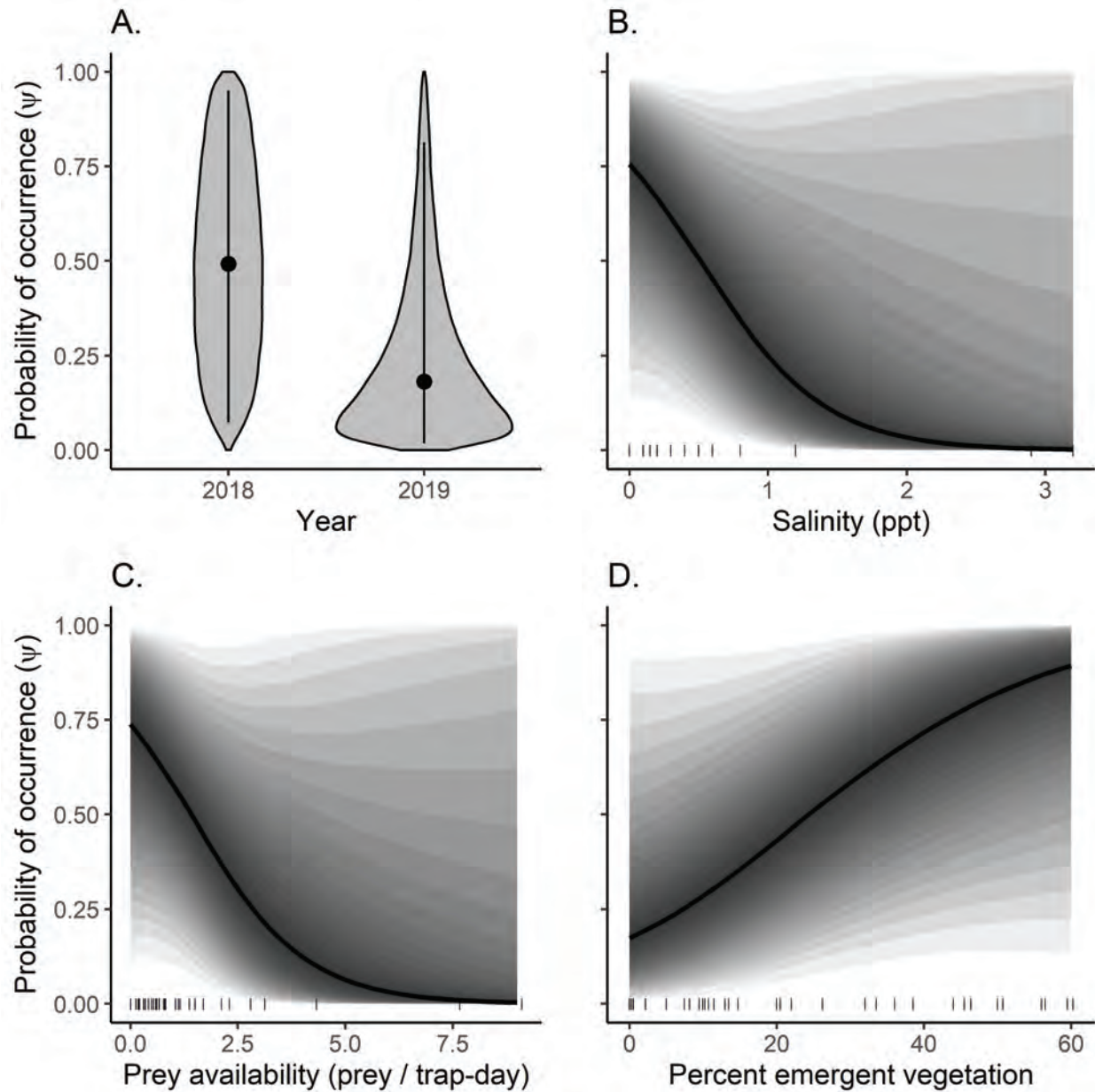


Figure 3. Effects of A, year; B, salinity; C, prey availability; and D, emergent vegetation cover on probability of occurrence of giant gartersnakes (*Thamnophis gigas*) in the Sacramento–San Joaquin Delta, California, 2018–19. In A, points represent posterior medians, lines represent 95-percent credible intervals, and shaded areas represent posterior distributions. In B–D, lines represent posterior medians; shading represents posterior distributions in 0.05 quantile bands, with the outermost bands representing 95-percent credible intervals; vertical lines along the x-axis indicate observed values.

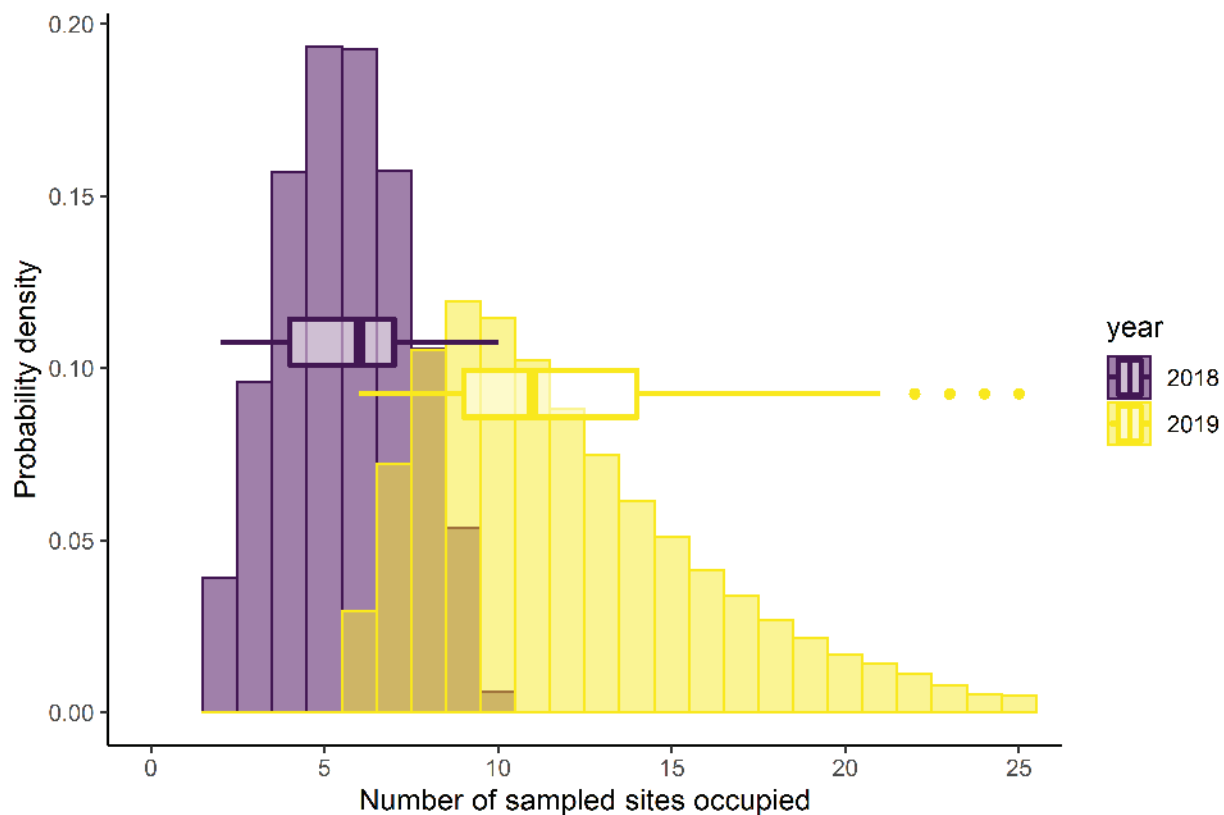


Figure 4. Posterior distribution of the number of sampled sites occupied by giant gartersnakes (*Thamnophis gigas*) in the Sacramento–San Joaquin Delta, California, 2018–19. The histogram represents the entire posterior distribution; the boxplot represents the median and interquartile range (IQR), whiskers represent 1.5 times IQR, and dots represent values beyond 1.5 times IQR.

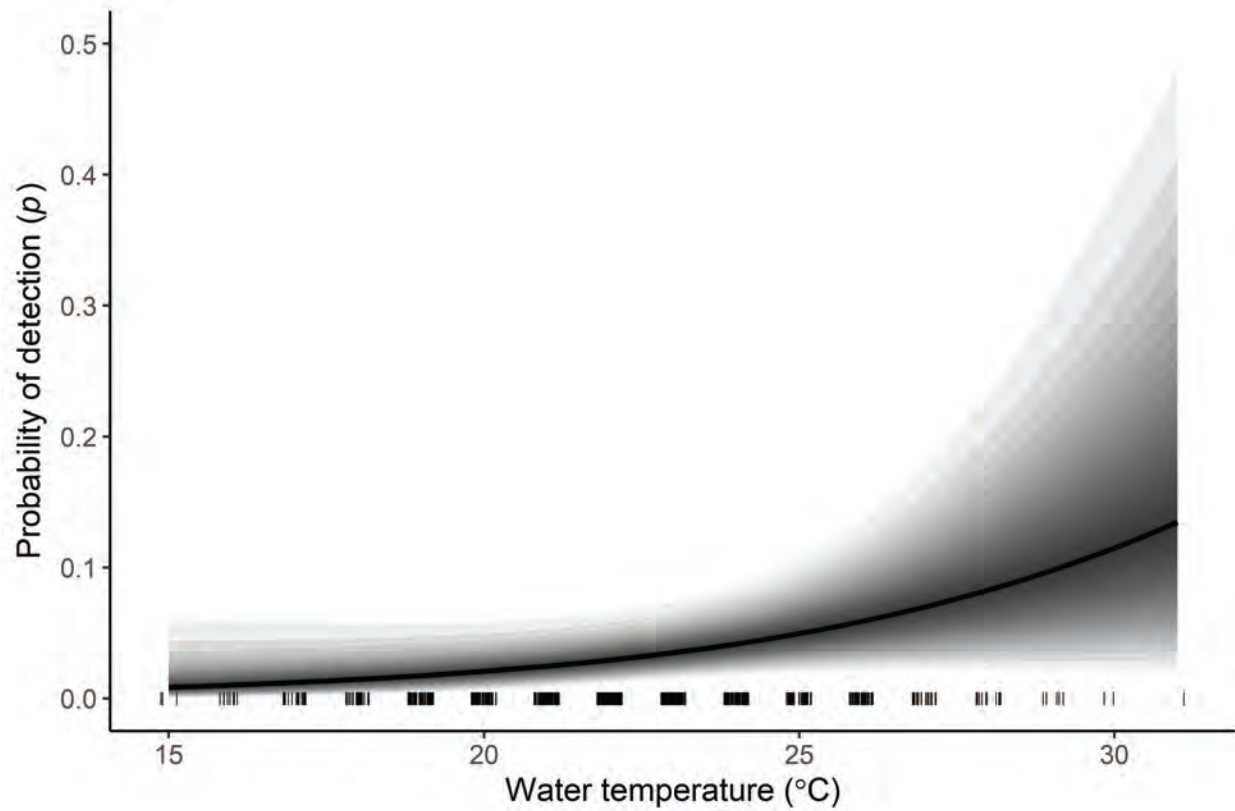


Figure 5. Effect of water temperature on giant gartersnake (*Thamnophis gigas*) detection probability in the Sacramento–San Joaquin Delta, California, 2018–19. The line represents the posterior median; shading represents the posterior distribution in 0.05 quantile bands, with the outermost bands representing 95-percent credible intervals; vertical lines along the x-axis indicate observed values jittered to reduce overplotting.

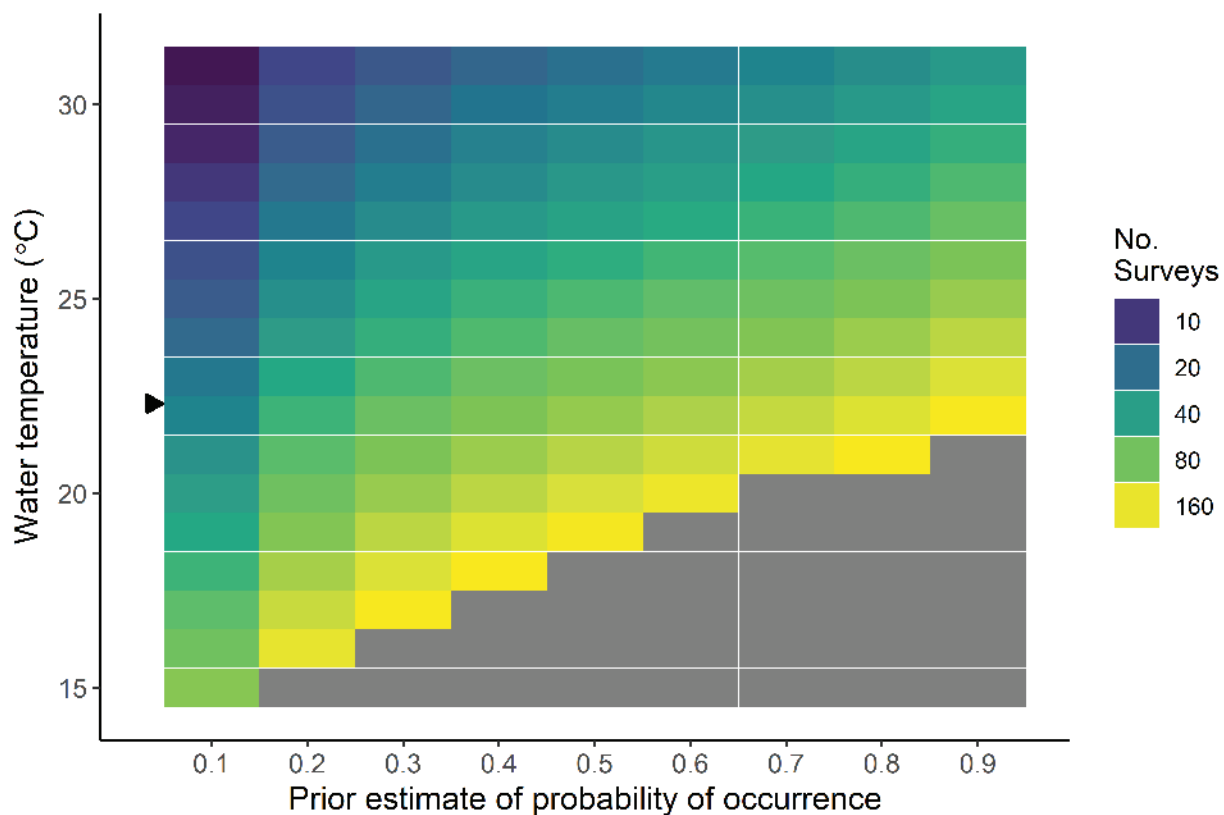


Figure 6. Median estimate of the number of consecutive non-detection surveys required to declare absence of giant gartersnakes (*Thamnophis gigas*) in the Sacramento–San Joaquin Delta with 95-percent certainty based on prior probability of occurrence and water temperature. The triangle along the y-axis indicates the observed mean water temperature during surveys completed in 2018–19. Gray values indicate median consecutive samples that are longer than 180 days or the length of a full field season.

Table 4. Summary of giant gartersnake (*Thamnophis gigas*), valley gartersnake (*Thamnophis sirtalis fitchi*), mountain gartersnake (*Thamnophis elegans elegans*), and Pacific gophersnake (*Pituophis catenifer catenifer*) captures in the Sacramento–San Joaquin Delta during summer 2018–19.

[—, not sampled]

Trapline	Giant gartersnakes		Valley gartersnakes		Mountain gartersnakes		Pacific gophersnakes	
	2018	2019	2018	2019	2018	2019	2018	2019
Bowlsbey 1	0	0	1	1	0	0	0	0
Bowlsbey 2	0	1	0	1	0	0	0	0
Liberty Farms 1	7	0	13	3	0	0	0	0
Liberty Farms 2	0	—	18	—	0	—	0	—
Liberty Farms 3	0	—	1	—	0	—	0	—
Liberty Farms 4	—	1	—	0	—	0	—	0
Liberty Farms 5	—	1	—	11	—	0	—	0
Sherman 1	—	0	—	0	—	0	—	1
Sherman 2	—	0	—	0	—	0	—	0
Sherman 3	—	0	—	0	—	0	—	0
Sherman 4	—	0	—	0	—	0	—	0
Sherman 5	—	1	—	0	—	0	—	0
Shin Kee 1	—	0	—	0	—	0	—	0
Shin Kee 2	—	1	—	0	—	0	—	0
Shin Kee 3	—	1	—	0	—	2	—	0
Staten 1	—	0	—	0	—	0	—	0
Staten 2	—	0	—	0	—	0	—	0
Staten 3	—	0	—	2	—	0	—	0
Staten 4	—	0	—	4	—	0	—	1
Staten 5	—	0	—	1	—	0	—	0
Twitchell 1	0	0	0	0	0	0	0	0
Twitchell 2	0	0	1	0	0	0	0	0
Twitchell 3	0	0	0	1	0	0	0	0
Twitchell 4	—	0	0	0	0	0	0	0
Twitchell 5	—	0	0	1	0	0	0	0
Yolo Flyway 1	1	0	0	2	0	0	0	0
Yolo Flyway 2	0	0	0	8	0	0	0	0
Total	8	6	34	35	0	2	0	2

Discussion

The main purpose of this study was to examine the distribution of giant gartersnakes in the Delta and evaluate the relationship that landscape-level habitat, local microhabitat, vegetation composition, and prey counts had with their occurrence. In particular, we sought to identify whether probability of occurrence was affected by emergent vegetation, salinity, and prey availability, while also accounting for the potential for false absences or failing to detect giant gartersnakes where they occur. Despite logistical difficulties and low detection probabilities, our study documented presence of giant gartersnakes at several sites and identified several variables that appear to be related to their distribution in the Delta. These variables included salinity, emergent vegetation cover, and relative abundance of fishes, frogs, and tadpoles. Interpreting the importance of these variables must be done with great caution because the credible intervals of the parameters of each variable overlapped zero. The most likely reason for the wide credible intervals is because we only captured giant gartersnakes at eight transects, and we strongly suspect they would become considerably narrower if we had more captures at more transects. Nonetheless, although we acknowledge the limitations the small number of captures imposes, we believe salinity, vegetation cover, and prey abundance are plausible ecological mechanisms related to distribution of giant gartersnakes in the Delta.

Salinity was negatively related to the probability of giant gartersnake occurrence. Estuarine and marine reptiles typically have behavioral or physiological adaptations to avoid highly saline environments or remove excess salt from the body (Dunson and Mazzotti, 1989). Freshwater natricine snakes in the eastern United States, when placed in sea water, lose water through the skin, drink the saline water, and, if not removed to a freshwater environment, die (Dunson, 1980). Giant gartersnakes, whose occurrence is primarily known from freshwater marshes, likely have a similar physiological and behavioral response to saline conditions as other freshwater snakes, and therefore are less likely to occur in areas with higher salinity. Because the maximum salinity in our study was relatively low (3 ppt), future studies along a larger salinity gradient would better evaluate the response of giant gartersnakes to salinity.

Based on radio telemetry studies, we expected the positive relationship we observed between emergent vegetation and giant gartersnake occurrence (Halstead and others, 2016). Previous trapping studies of the occurrence of giant gartersnakes, however, have found no evidence for a relationship between emergent vegetation cover and occurrence (Halstead and others, 2014, 2015a). At the individual level, giant gartersnakes select emergent vegetation, especially hardstem bulrush, in preference to other available substrates (Halstead and others, 2016). Emergent aquatic vegetation provides cover from predators (Halstead and others, 2016; Emmons, 2017; Sprague and Bateman, 2018), such as raptors, large wading birds, large bullfrogs, large fish, and

nocturnal mammals such as raccoons, skunks, and opossums. Indeed, the extreme wariness of giant gartersnakes has been attributed to high predator abundance combined with the open habitat conditions to which these snakes are exposed (Fitch, 1940). Emergent vegetation, especially hardstem bulrush, also provides good basking substrate for giant gartersnakes. Its growth above the water surface allows snakes to bask in air and elevate their body temperatures (Halstead and others, 2016; Emmons, 2017; Sprague and Bateman, 2018), yet it allows them to flee quickly into the water if threatened by predators.

In contrast to our expectations, giant gartersnake occurrence was negatively related to prey relative abundance. Because we broadly defined prey as American bullfrogs and their tadpoles, Sierran treefrogs (*Pseudacris sierra*) and their tadpoles, and a variety of fish species, “prey” likely included small individuals of potential predators, especially bullfrogs and predatory fishes. In addition, giant gartersnakes likely have complex predator-prey relationships because of reciprocal intraguild predation (Marques and others, 2018; Kim and others, 2020). For example, adult giant gartersnakes eat small bullfrogs and fish (Ersan and others, 2020a), and large bullfrogs and fish eat small giant gartersnakes (Wylie and others, 2003). In the Delta, the possibility also exists that large fish not typically occurring elsewhere in the giant gartersnake’s range could eat adult giant gartersnakes. Refining our examination of gartersnake occurrence in the future by using individual prey species could reveal which species are positively or negatively related to occurrence. It also is possible that fewer prey lead to more active foraging, which leads to higher detection probabilities; however, because of few detections of giant gartersnakes, we could not adequately evaluate this possibility in this study.

Detection probabilities were an order of magnitude lower in the Delta (0.03 [0.01–0.07]) than in the Sacramento Valley, where recent (2016–19) mean detection probabilities using the same traps and effort have ranged from 0.21 (0.10–0.40) to 0.55 (0.33–0.77). This large difference could be attributed to several factors. First, water temperature and detection probability are positively related in both the Delta and Sacramento Valley (Halstead and others, 2011, 2014). This relationship is likely because warmer water allows giant gartersnakes, which are ectothermic, to spend more time in the water foraging before their body temperature drops to the point where they need to leave the water to bask. Mean and maximum water temperatures in the Delta (22.3 and 31 °C, respectively) were lower than that in the Sacramento Valley (23.3 and 35 °C, respectively), likely reducing aquatic activity and detection probability in the Delta. At higher water temperatures, detection probabilities might decrease following a quadratic relationship. We did not fit a quadratic effect of water temperature on detection probability because the maximum observed water temperature was approximately equal to the field-preferred body temperature of giant gartersnakes in the Sacramento Valley (29.8 [27.6–31.7] °C; Wylie and others, 2009).

Another variable that is usually related to detection probabilities is the density of the species of interest. The more individuals that are available to be detected, generally the higher the detection probability (Royle and Nichols, 2003). It is possible that giant gartersnakes occur in lower densities in the Delta than in the Sacramento Valley, which would likely lead to lower detection probabilities in the Delta. Our capture rates of valley gartersnakes in our aquatic traps were much higher than our capture rates of more aquatic giant gartersnakes, supporting the idea that giant gartersnake densities at occupied sampled sites were low. We are currently collecting data in the Sacramento Valley that could allow us to explicitly evaluate the relationship between density and detection probability for giant gartersnakes to better evaluate this relationship. Other variables that might account for differences in detection probabilities between the Sacramento Valley and Delta include differences in behavior or habitat use that cause snakes to be more or less likely to encounter traps, though again we note that we captured valley gartersnakes at 4–6 times the rate at which we captured giant gartersnakes, suggesting that our traps were effective at capturing gartersnakes in many instances.

The low detection probability of giant gartersnakes in the Delta increases uncertainty about their status in the region. Low detection probabilities are not uncommon in snakes (Durso and others, 2011), and it is important to account for imperfect detection when interpreting surveys that fail to detect snakes. For only a few combinations of water temperature and prior probability of occurrence would failure to detect giant gartersnakes, given our sampling effort (50 traps set for 21 consecutive days, or 1,050 trap-days), result in the ability to state with 95-percent certainty that giant gartersnakes were absent from a site. Indeed, with a prior probability of occurrence greater than 0.5 or water temperatures below 23 °C, one would require more than 21 consecutive days of non-detections to declare absence of giant gartersnakes. In many realistic sampling situations, one could not declare absence with 95-percent certainty even if sampling occurred throughout the entire mid-April through late September active season. Furthermore, the lowest posterior probability a site was occupied by giant gartersnakes in our study was 0.11 (table 1). Improving inference about the occurrence of giant gartersnakes in the Delta will therefore require improved methods for detecting these snakes in this region. Further development and validation of eDNA methods (Halstead and others, 2017; Schumer and others, 2019), detection dogs, or other methods of detecting giant gartersnakes in the Delta might improve detection probabilities and therefore inference about the occurrence of giant gartersnakes there.

In addition to low detection probabilities, several other challenges affected our study of giant gartersnakes in the Delta. Identifying landowners at randomly selected sites, then gaining permission to sample those sites, was more difficult than anticipated. Having not worked in the Delta previously,

we did not have the same degree of landowner contacts that we had acquired through decades of work in the Sacramento Valley. We initially used ParcelQuest to identify landowners, but much of the contact information for landowners was incomplete or out of date. Often, landowners did not respond to our queries; indeed, the lack of a response was the primary obstacle, because we received only one absolute negative response. When the landowner was an agency or organization, the appropriate contact person often was not obvious, causing further delays in obtaining permission. Because of this difficulty, we had to abandon random sampling in 2019 and instead sample opportunistically at sites where permission was easier to obtain, but even without attempting a truly random sample, obtaining permission to sample remained an obstacle to gaining the access required for obtaining inference across the Delta. We did have increased success after being put in contact with the San Joaquin Council of Governments, but unfortunately, we were unaware of this potential source of information until late in the project. Future giant gartersnake studies in the Delta would benefit by increasing effort to identify and contact landowners well in advance of fieldwork. Assistance from regulatory and resource management agencies before project implementation likely would improve landowner buy-in for projects because such efforts (for example, by the USFWS, Bureau of Reclamation, and California Department of Water Resources) have been instrumental for obtaining access to conduct studies on private lands in the Sacramento Valley.

We also had to abandon some sites because of tides. Tides affect giant gartersnake traps in several ways. Our traps float and are set with the intention that they will move vertically with the increasing and decreasing water levels at a small scale; however, the change in water levels in tidal areas can be too drastic for our trapping system. Vertical movement of the water caused by tides could endanger snakes by drowning when increasing water levels submerge traps or overheating when decreasing water levels strand traps. We abandoned two potential sites because of the potential danger they posed to trapped snakes. In addition to vertical water movement, the changing direction of tidal flows pushes and pulls the traps, moving them away from the shoreline or edge of emergent vegetation where they are most effective, thereby decreasing detection probabilities.

Despite these challenges, this study has furthered our understanding of giant gartersnake ecology in the Delta. We confirmed giant gartersnake occurrence at a number of sites and have some evidence that salinity, emergent vegetation cover, and relative abundance of prey influence giant gartersnake occurrence. In particular, freshwater sites with more cover in our sample are more likely to be occupied by giant gartersnakes, but a better understanding of the complex size-structured predator-prey relationships of giant gartersnakes with bullfrogs and fish would improve our understanding of giant gartersnakes' response to differences in potential prey communities.

By quantifying the low detection probabilities of giant gartersnakes in traps in the Delta, we were able to calculate the survey effort necessary to declare absence of giant gartersnakes from a site at a given level of certainty. Using current trapping protocols developed in the Sacramento Valley, the level of effort required to declare absence of giant gartersnakes from a site with 95-percent certainty is infeasible, and further development of sampling methods to improve giant gartersnake detection probabilities in the Delta is warranted. Despite progress made in this study, much remains to be learned about giant gartersnakes in the unique Sacramento–San Joaquin Delta ecosystem.

Summary

- We examined the occurrence of giant gartersnakes in the Sacramento–San Joaquin Delta, California, in 2018 and 2019.
- We made eight captures of seven giant gartersnakes (three females, four males) in 2018, and six captures of six giant gartersnakes (four females, two males) in 2019.
- Detection probabilities were exceedingly low despite using methods that achieve much higher detection probabilities in the rice-growing regions of the Sacramento Valley, California.
- Our results indicated negative effects of salinity and prey abundance and positive effects of percent emergent vegetation on giant gartersnake occurrence in the Delta, but credible intervals of effect sizes broadly overlapped zero.
- Estimates of giant gartersnake probability of occurrence were characterized by substantial uncertainty.
- Additional study with a larger sample of randomly selected but accessible sites would help to further resolve the distribution of giant gartersnakes in the Delta and clarify how the physical and biotic environment in the Delta affects where giant gartersnakes exist.
- Methodological development to increase detection probabilities in the Delta also would improve inference about giant gartersnake occupancy in the region.

References Cited

- California Department of Fish and Game Commission, 1971, Animals of California declared to be endangered or threatened: Sacramento, Calif., California Department of Fish and Game Commission.
- Dunson, W.A., 1980, The relation of sodium and water balance to survival in sea water of estuarine and freshwater races of the snakes *Nerodia fasciata*, *N. sipedon*, and *N. valida*: *Copeia*, v. 1980, no. 2, p. 268–280, <https://doi.org/10.2307/1444004>.
- Dunson, W.A., and Mazzotti, F.J., 1989, Salinity as a limiting factor in the distribution of reptiles in Florida Bay—A theory for the estuarine origin of marine snakes and turtles: *Bulletin of Marine Science*, v. 44, no. 1, p. 229–244.
- Durso, A.M., Willson, J.D., and Winne, C.T., 2011, Needles in haystacks—Estimating detection probability and occupancy of rare and cryptic snakes: *Biological Conservation*, v. 144, no. 5, p. 1508–1515, <https://doi.org/10.1016/j.biocon.2011.01.020>.
- Emmons, I.D., 2017, Ecology of federally threatened northern Mexican gartersnakes in north-central Arizona: Flagstaff, Arizona, Northern Arizona University, M.S. thesis.
- Ersan, J.S.M., Halstead, B.J., Wildy, E.L., Casazza, M.L., and Wylie, G.D., 2020a, Giant gartersnakes (*Thamnophis gigas*) exploit abundant nonnative prey while maintaining their appetite for native anurans: *Herpetologica*, v. 76, no. 3, p. 290–296, <https://doi.org/10.1655/Herpetologica-D-18-00026.1>.
- Ersan, J.S.M., Halstead, B.J., Wildy, E.L., Casazza, M.L., and Wylie, G.D., 2020b, Intrinsic prey preference of the giant gartersnake—A threatened predator in a nonnative prey-dominated community: *Journal of Fish and Wildlife Management*, v. 11, no. 1, p. 164–173, <https://doi.org/10.3996/062019-JFWM-051>.
- Fitch, H.S., 1940, A biogeographical study of the ordinoides artenkreis of garter snakes (genus *Thamnophis*): University of California Publications in Zoology, v. 44, no. 1, p. 1–150.
- Gelman, A., and Rubin, D.B., 1992, Inference from iterative simulation using multiple sequences: *Statistical Science*, v. 7, no. 4, p. 457–472, <https://doi.org/10.1214/ss/1177011136>.

- Halstead, B.J., Wylie, G.D., and Casazza, M.L., 2010, Habitat suitability and conservation of the giant gartersnake (*Thamnophis gigas*) in the Sacramento Valley of California: Copeia, v. 2010, no. 4, p. 591–599, <https://doi.org/10.1643/CE-09-199>.
- Halstead, B.J., Wylie, G.D., Coates, P.S., and Casazza, M.L., 2011, Bayesian adaptive survey protocols for resource management: The Journal of Wildlife Management, v. 75, no. 2, p. 450–457, <https://doi.org/10.1002/jwmg.55>.
- Halstead, B.J., Wylie, G.D., and Casazza, M.L., 2013, Efficacy of trap modifications for increasing capture rates of aquatic snakes in floating aquatic funnel traps: Herpetological Conservation and Biology, v. 8, no. 1, p. 65–74.
- Halstead, B.J., Wylie, G.D., and Casazza, M.L., 2014, Ghost of habitat past—Historic habitat affects the contemporary distribution of giant garter snakes in a modified landscape: Animal Conservation, v. 17, no. 2, p. 144–153, <https://doi.org/10.1111/acv.12073>.
- Halstead, B.J., Skalos, S.M., Casazza, M.L., and Wylie, G.D., 2015a, A preliminary investigation of the variables affecting the distribution of giant gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California: U.S. Geological Survey Open-File Report 2015–1178, 34 p., <https://doi.org/10.3133/ofr20151178>.
- Halstead, B.J., Skalos, S.M., Wylie, G.D., and Casazza, M.L., 2015b, Terrestrial ecology of semi-aquatic giant gartersnakes (*Thamnophis gigas*): Herpetological Conservation and Biology, v. 10, no. 2, p. 633–644.
- Halstead, B.J., Wylie, G.D., and Casazza, M.L., 2015c, Literature review of giant gartersnake (*Thamnophis gigas*) biology and conservation: U.S. Geological Survey Open-File Report 2015–1150, 38 p., <https://doi.org/10.3133/ofr20151150>.
- Halstead, B.J., Valcarcel, P., Wylie, G.D., Coates, P.S., Casazza, M.L., and Rosenberg, D.K., 2016, Active season microhabitat and vegetation selection by giant gartersnakes associated with a restored marsh in California: Journal of Fish and Wildlife Management, v. 7, no. 2, p. 397–407, <https://doi.org/10.3996/042016-JFWM-029>.
- Halstead, B.J., Wood, D.A., Bowen, L., Waters, S.C., Vandergast, A.G., Ersan, J.S., Skalos, S.M., and Casazza, M.L., 2017, An evaluation of the efficacy of using environmental DNA (eDNA) to detect giant gartersnakes (*Thamnophis gigas*): U.S. Geological Survey Open-File Report 2017–1123, 41 p., <https://doi.org/10.3133/ofr20171123>.
- Halstead, B.J., Rose, J.P., Reyes, G.A., Wylie, G.D., and Casazza, M.L., 2019, Conservation reliance of a threatened snake on rice agriculture: Global Ecology and Conservation, v. 19, 11 p., <https://doi.org/10.1016/j.gecco.2019.e00681>.
- Hansen, G.E., 1986, Status of the giant garter snake *Thamnophis couchi gigas* (Fitch) in the southern Sacramento Valley during 1986: Final Report to California Department of Fish and Game, 28 p.
- Hansen, E.C., Scherer, R.D., White, G.C., Dickson, B.G., and Fleishman, E., 2015, Estimates of survival probability from two populations of giant gartersnakes in California's Great Central Valley: Copeia, v. 103, no. 4, p. 1026–1036, <https://doi.org/10.1643/CE-15-233>.
- Hansen, E.C., Scherer, R.D., Fleishman, E., Dickson, B.G., and Krolick, D., 2017, Relations between environmental attributes and contemporary occupancy of threatened giant gartersnakes (*Thamnophis gigas*): Journal of Herpetology, v. 51, no. 2, p. 274–283, <https://doi.org/10.1670/16-143>.
- Kellner, K., 2018, Package “jagsUI”—A wrapper around ‘rjags’ to streamline ‘JAGS’ analyses: R package version 1.5.0.
- Kéry, M., 2010, Introduction to WinBUGS for ecologists—A bayesian approach to regression, ANOVA, mixed models and related analyses: Burlington, Mass., Academic Press, 320 p.
- Kéry, M., and Royle, J.A., 2016, Applied hierarchical modeling in ecology—Analysis of distribution, abundance, and species richness in R and BUGS—Volume 1—Prelude and static models: Academic Press, London, UK, 783 p.
- Kim, R., Halstead, B.J., Routman, E.J., and Andersen, J., 2020, (in press) When introduced prey violates trophic hierarchy—Conservation of an endangered predator: Biological Conservation.
- Kincaid, T.M., and Olsen, A.R., 2016, spsurvey—Spatial survey design and analysis: R package version 3.3.
- Link, W.A., and Barker, R.J., 2010, Bayesian inference—With ecological applications: London, UK, Academic Press, 339 p.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., and Langtimm, C.A., 2002, Estimating site occupancy rates when detection probabilities are less than one: Ecology, v. 83, no. 8, p. 2248–2255, [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2).
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E., 2006, Occupancy estimation and modeling—Inferring patterns and dynamics of species occurrence: Amsterdam, The Netherlands, Academic Press, 344 p.

- Marques, R.V., Sarmiento, R.A., Oliveira, A.G., Rodrigues, D.M., Venzon, M., Pedro-Neto, M., Pallini, A., and Janssen, A., 2018, Reciprocal intraguild predation and predator coexistence: Ecology and Evolution, v. 8, no. 14, p. 6952–6964, <https://doi.org/10.1002/ece3.4211>.
- Plummer, M., 2017, JAGS Version 4.3.0 user manual: JAGS, 73 p.
- R Core Team, 2019, R—A language and environment for statistical computing: R Foundation for Statistical Computing, Vienna, Austria.
- Rose, J.P., Ersan, J.S.M., Wylie, G.D., Casazza, M.L., and Halstead, B.J., 2018a, Reproductive frequency and size-dependence of fecundity in the giant gartersnake (*Thamnophis gigas*): Herpetological Conservation and Biology, v. 13, no. 1, p. 80–90.
- Rose, J.P., Halstead, B.J., Wylie, G.D., and Casazza, M.L., 2018b, Spatial and temporal variability in growth of giant gartersnakes—Plasticity, precipitation, and prey: Journal of Herpetology, v. 52, no. 1, p. 40–49, <https://doi.org/10.1670/17-055>.
- Rose, J.P., Wylie, G.D., Casazza, M.L., and Halstead, B.J., 2018c, Integrating growth and capture–mark–recapture models reveals size-dependent survival in an elusive species: Ecosphere, v. 9, no. 8, 18 p., <https://doi.org/10.1002/ecs2.2384>.
- Rose, J.P., Ersan, J.S.M., Wylie, G.D., Casazza, M.L., and Halstead, B.J., 2019, Demographic factors affecting population growth in giant gartersnakes: The Journal of Wildlife Management, v. 83, no. 7, p. 1540–1551, <https://doi.org/10.1002/jwmg.21728>.
- Rossman, D.A., Ford, N.B., and Seigel, R.A., 1996, The garter snakes—Evolution and ecology: Norman, Oklahoma, USA, University of Oklahoma Press, 336 p.
- Royle, J.A., and Dorazio, R.M., 2008, Hierarchical modeling and inference in ecology—The analysis of data from populations, metapopulations and communities: London, UK, Academic Press, 444 p.
- Royle, J.A., and Nichols, J.D., 2003, Estimating abundance from repeated presence-absence data or point counts: Ecology, v. 84, no. 3, p. 777–790, [https://doi.org/10.1890/0012-9658\(2003\)084\[0777:EAFRPA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2).
- Schumer, G., Hansen, E.C., Anders, P.J., and Blankenship, S.M., 2019, Development of a quantitative polymerase chain reaction assay and environmental DNA sampling methods for giant gartersnake (*Thamnophis gigas*): PLoS One, v. 14, no. 9, 13 p., <https://doi.org/10.1371/journal.pone.0222493>.
- Sprague, T.A., and Bateman, H.L., 2018, Influence of seasonality and gestation on habitat selection by northern Mexican gartersnakes (*Thamnophis eques megalops*): PLoS One, v. 13, no. 1, 23 p., <https://doi.org/10.1371/journal.pone.0191829>.
- Stevens, D.L., Jr., and Olsen, A.R., 2004, Spatially balanced sampling of natural resources: Journal of the American Statistical Association, v. 99, no. 465, p. 262–278, <https://doi.org/10.1198/016214504000000250>.
- Thompson, W.L., MacKenzie, D.I., Royle, J.A., Brown, J.A., Nichols, J.D., and Thompson, W.L., 2004, Occupancy estimation and modeling for rare and elusive populations, in Thompson, W.L., ed., Sampling rare or elusive populations—Concepts, designs, and techniques for estimating population parameters: Washington, D.C., USA, Island Press, p. 149–172.
- U.S. Fish and Wildlife Service, 1993, Endangered and threatened wildlife and plants; Determination of threatened status for the giant garter snake (*Thamnophis gigas*): Federal Register, v. 58, no. 201, p. 54053–54066.
- Winne, C.T., Willson, J.D., Andrews, K.M., and Reed, R.N., 2006, Efficacy of marking snakes with disposable medical cautery units: Herpetological Review, v. 37, no. 1, p. 52–54.
- Wintle, B.A., Walshe, T.V., Parris, K.M., and McCarthy, M.A., 2012, Designing occupancy surveys and interpreting non-detection when observations are imperfect: Diversity & Distributions, v. 18, no. 4, p. 417–424, <https://doi.org/10.1111/j.1472-4642.2011.00874.x>.
- Wood, D.A., Halstead, B.J., Casazza, M.L., Hansen, E.C., Wylie, G.D., and Vandergast, A.G., 2015, Defining population structure and genetic signatures of decline in the giant gartersnake (*Thamnophis gigas*)—Implications for conserving threatened species within highly altered landscapes: Conservation Genetics, v. 16, no. 5, p. 1025–1039, <https://doi.org/10.1007/s10592-015-0720-6>.
- Wylie, G.D., Casazza, M.L., and Carpenter, N.M., 2003, Diet of bullfrogs in relation to predation on giant garter snakes at Colusa National Wildlife Refuge: California Fish and Game, v. 89, no. 3, p. 139–145.
- Wylie, G.D., Casazza, M.L., Halstead, B.J., and Gregory, C.J., 2009, Sex, season, and time of day interact to affect body temperatures of the giant gartersnake: Journal of Thermal Biology, v. 34, no. 4, p. 183–189, <https://doi.org/10.1016/j.jtherbio.2009.01.006>.

Appendix 1. Supplemental Figures

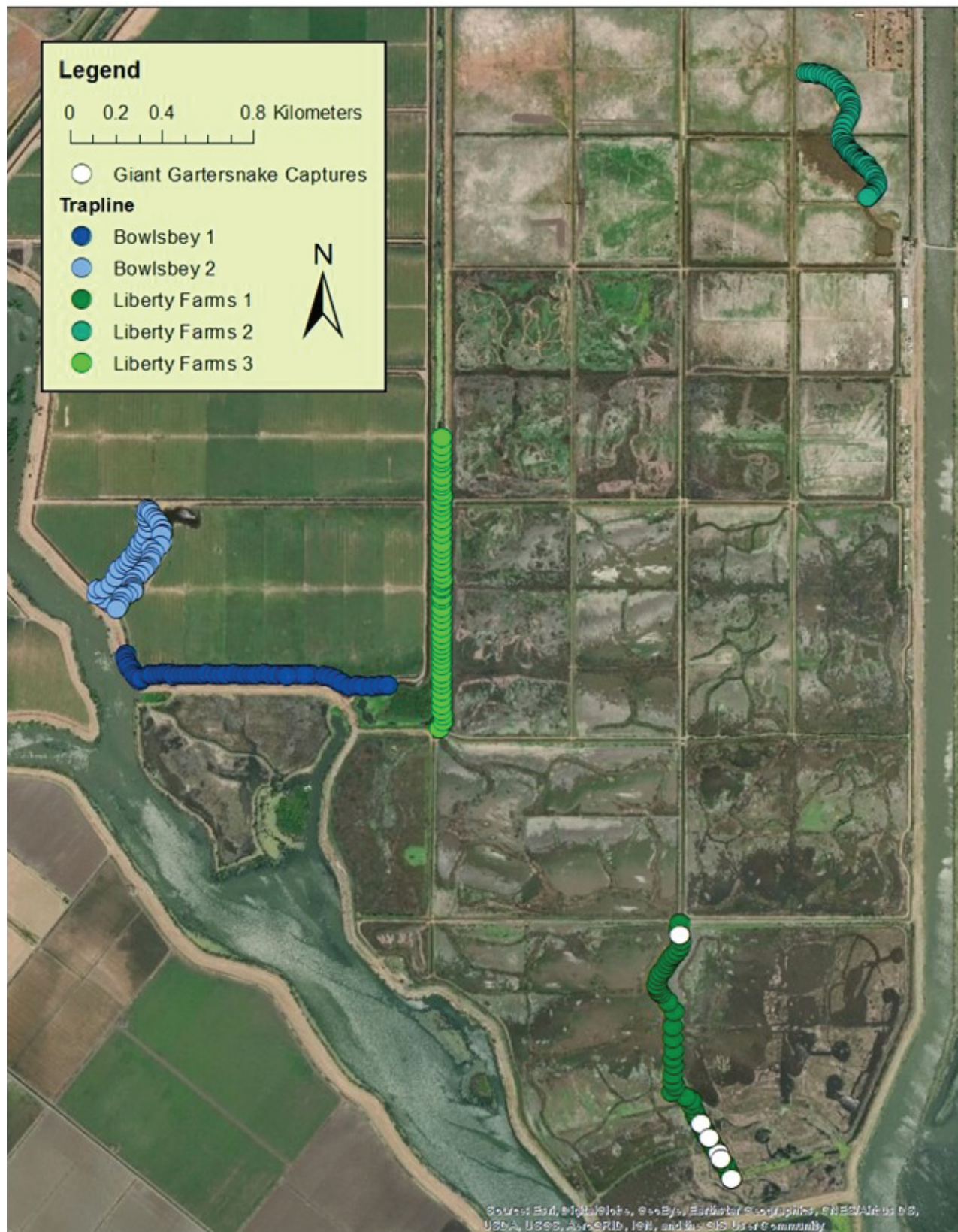


Figure 1.1. Location of giant gartersnake (*Thamnophis gigas*) traps and captures at Bowsbey Ranch and Liberty Farms in 2018.



Figure 1.2. Location of giant gartersnake (*Thamnophis gigas*) traps and capture at Yolo Flyway in 2018.



Figure 1.3. Location of giant gartersnake (*Thamnophis gigas*) traps at Twitchell Island in 2018.



Figure 1.4. Location of giant gartersnake (*Thamnophis gigas*) traps and captures at Bowsbey Ranch and Liberty Farms in 2019.



Figure 1.5. Locations of giant gartersnake (*Thamnophis gigas*) traps and capture at Sherman Island in 2019.

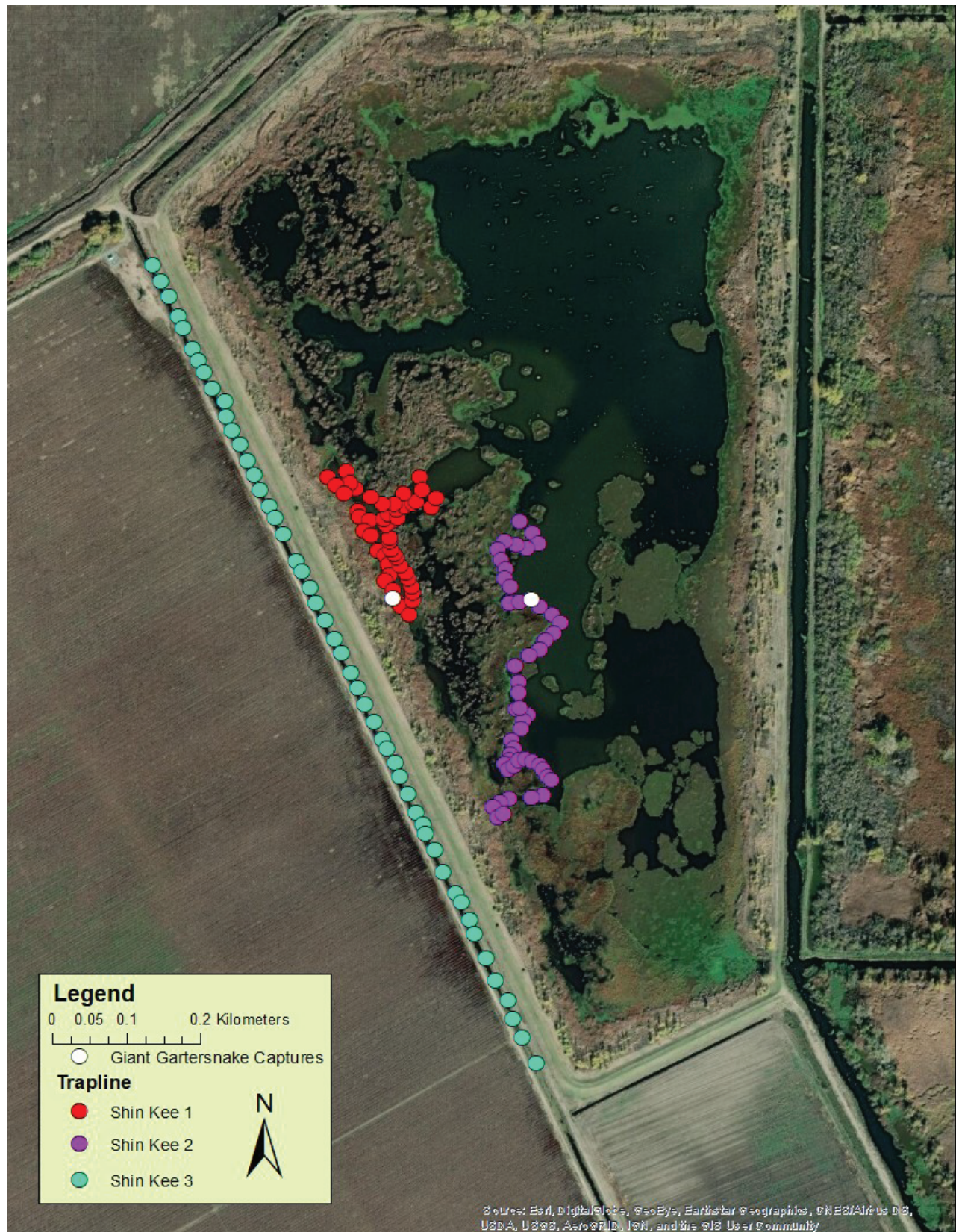


Figure 1.6. Locations of giant gartersnake (*Thamnophis gigas*) traps and captures at Shin Kee in 2019.

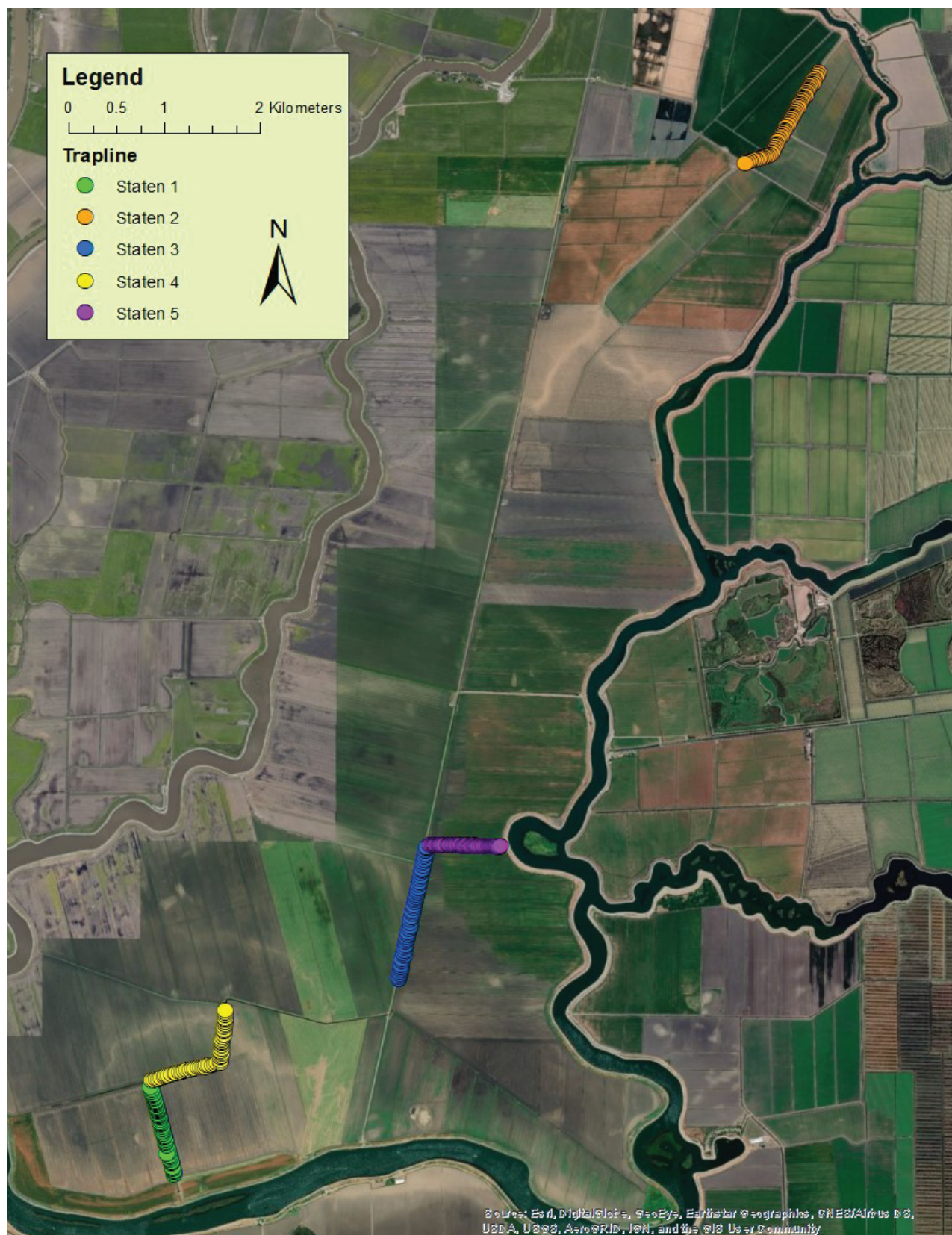


Figure 1.7. Locations of giant gartersnake (*Thamnophis gigas*) traps at Staten Island in 2019.

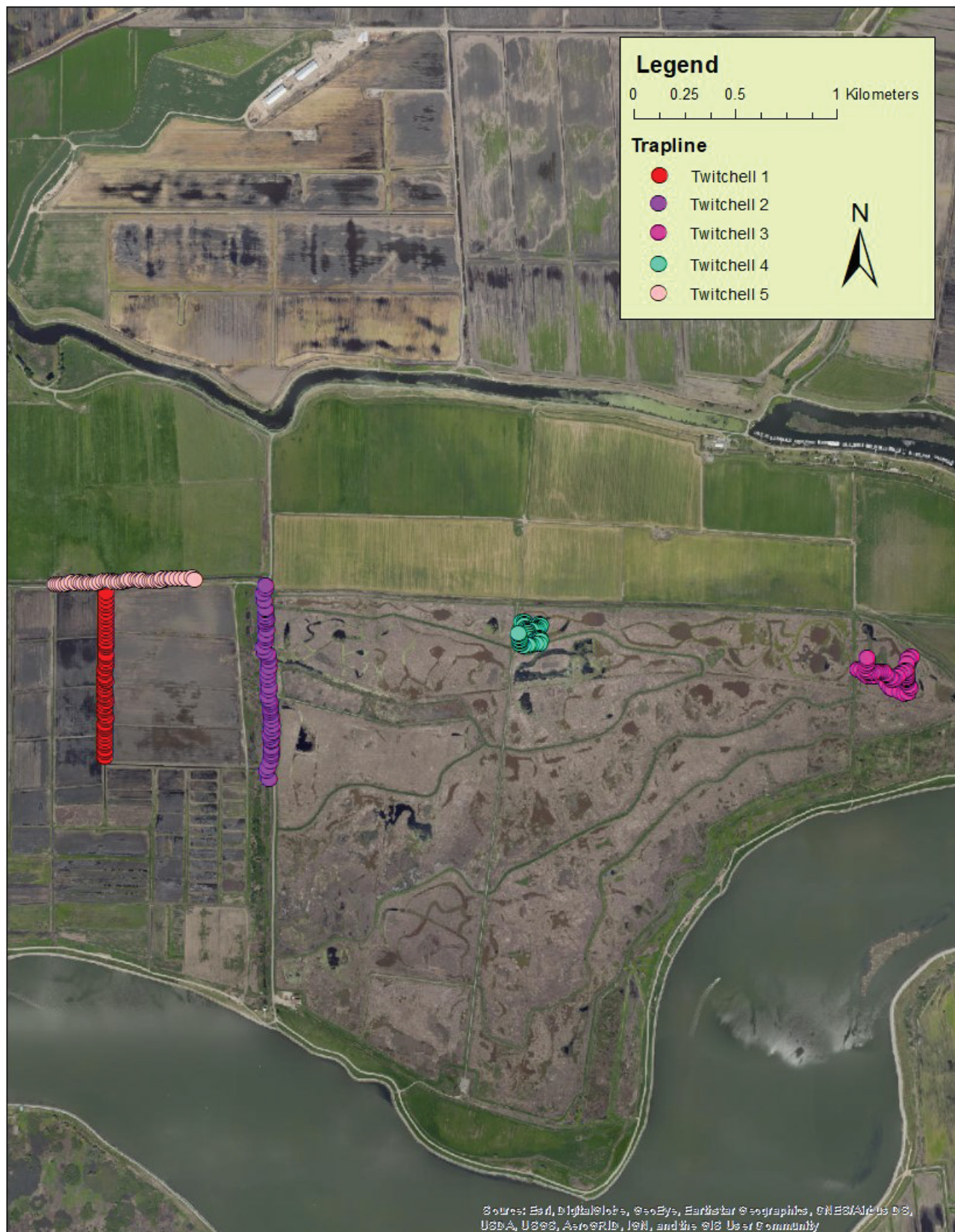


Figure 1.8. Locations of giant gartersnake (*Thamnophis gigas*) traps at Twitchell Island in 2019.



Figure 1.9. Locations of giant gartersnake (*Thamnophis gigas*) traps at Yolo Flyway in 2019.

For more information concerning the research in this report, contact the
Director, Western Ecological Research Center
U.S. Geological Survey
3020 State University Drive East
Sacramento, California 95819
<https://www.usgs.gov/centers/werc>
Publishing support provided by the U.S. Geological Survey
Science Publishing Network, Sacramento Publishing Service Center

