

Prepared in cooperation with the Midpeninsula Regional Open Space District

Distribution and Demography of San Francisco Gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California



Open-File Report 2018–1063

Cover: Photograph showing an adult San Francisco gartersnake (*Thamnophis sirtalis tetrataenia*) foraging in a wetland. U.S. Geological Survey photograph taken by Richard Kim.

Distribution and Demography of San Francisco Gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California

By Richard Kim, Brian J. Halstead, Glenn D. Wylie, and Michael L. Casazza

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Conversion Factors

U.S. customary units to International System of Units

Multiply	By	To obtain
Area		
acre	0.4047	hectare (ha)
acre	0.4047	square hectometer (hm ²)

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)
meter (m)	1.094	yard (yd)
Area		
hectare (ha)	2.471	acre
square hectometer (hm ²)	2.471	acre
square hectometer (hm ²)	0.003861	section (640 acres or 1 square mile)
hectare (ha)	0.003861	square mile (mi ²)
Mass		
gram (g)	0.03527	ounce, avoirdupois (oz)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as °F = (1.8 × °C) + 32.

Datum

Horizontal coordinate information is referenced to the North American Datum of 1983 (NAD 83).

Abbreviations

CMR	capture-mark-recapture
JAGS	Just Another Gibbs Sampler
MCMC	Markov chain Monte Carlo
MROSD	Midpeninsula Regional Open Space District
SVL	snout-vent length

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Abstract

San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) are a subspecies of common gartersnakes endemic to the San Francisco Peninsula of northern California. Because of habitat loss and collection for the pet trade, San Francisco gartersnakes were listed as endangered under the precursor to the Federal Endangered Species Act. A population of San Francisco gartersnakes resides at Mindego Ranch, San Mateo County, which is part of the Russian Ridge Open Space Preserve owned and managed by the Midpeninsula Regional Open Space District (MROSD). Because the site contained non-native fishes and American bullfrogs (*Lithobates catesbeianus*), MROSD implemented management to eliminate or reduce the abundance of these non-native species in 2014. We monitored the population using capture-mark-recapture techniques to document changes in the population during and following management actions. Although drought confounded some aspects of inference about the effects of management, prey and San Francisco gartersnake populations generally increased following draining of Aquatic Feature 3. Continued management of the site to keep invasive aquatic predators from recolonizing or increasing in abundance, as well as vegetation management that promotes heterogeneous grassland/shrubland near wetlands, likely would benefit this population of San Francisco gartersnakes.

Introduction

Background

San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) are a subspecies of common gartersnakes, *Thamnophis sirtalis*, that are listed as endangered under both the California (California Fish and Game Commission, 1971) and Federal Endangered Species Acts (U.S. Department of the Interior, 1967), and are designated as a Fully Protected Species under the California Fish and Game Code (U.S. Fish and Wildlife Service 1985, 2006). The primary threats that led to the listing of San Francisco gartersnakes were the loss and adverse modification of wetlands and adjacent upland habitat by urbanization and commercial development, as well as agricultural conversion, stream and creek channelization, removal of emergent riparian vegetation, and riprapping of streambanks and shorelines (U.S. Fish and Wildlife Service 1985, 2006). Illegal collection of San Francisco gartersnakes and decreases in native anuran prey are additional threats (U.S. Fish and Wildlife Service, 1985, 2006).

Although non-native species also might be a threat to San Francisco gartersnakes, no consensus exists for the effects of invasive American bullfrogs (*Lithobates catesbeianus*) or introduced fishes on San Francisco gartersnakes (Barry 1994, 1996; Kupferberg, 1997; Boone and others, 2004; U.S. Fish and Wildlife Service, 2006; Biosearch Associates, 2012; Barry and Fellers, 2013).

No progress to secure habitat for the snakes or to set aside a refuge specifically for them had been made until 1978; 23 of 28 extant populations reported in 1978 were subject to human disturbance or threatened with destruction (U.S. Fish and Wildlife Service, 1985). The recovery priority for San Francisco gartersnakes is one of the highest ratings for a federally listed subspecies (U.S. Fish and Wildlife Service, 2006), yet few data are available regarding population trends and demographic characteristics of San Francisco gartersnakes.

The Recovery Plan for the San Francisco Garter Snake (U.S. Fish and Wildlife Service, 1985, 2006) initially focused on the protection of six significant existing populations and the creation of four new populations at undefined sites. The six locations were (1) West of Bayshore (San Francisco International Airport), (2) San Francisco State Fish and Game Refuge (San Francisco Public Utilities Commission), (3) Laguna Salada/Mori Point (City of San Francisco/National Park Service), (4) Pescadero Marsh and (5) Año Nuevo State Reserves (California State Parks), and (6) Cascade Ranch (private land owner; U.S. Fish and Wildlife Service, 2006). The species may be downlisted from endangered to threatened if 200 or more adults are maintained at a 1:1 sex ratio at each of the six existing locations for five consecutive years; if these numbers can be maintained at each of 10 locations for 15 consecutive years, then the species will be eligible for delisting (U.S. Fish and Wildlife Service, 1985).

The development of conservation plans for San Francisco gartersnakes has been hampered by a shortage of literature that applies robust statistical methods to address management questions. These snakes are cryptic and rarely encountered; therefore, inconsistent sampling efforts and study designs that do not account for imperfect detection inform little about their demography (Reeder and others, 2015). Little has been published about the demography of San Francisco gartersnakes (Halstead and others, 2011; Reeder and others, 2015), and no peer-reviewed literature is available to evaluate the effects of habitat management and invasive-species control on this endangered species. Statistically robust studies providing information about habitat requirements, foraging ecology, and demography are imperative for developing conservation and management plans for San Francisco gartersnakes.

San Francisco Gartersnake Biology

San Francisco gartersnakes are present only on the San Francisco peninsula in San Mateo County and the northern part of Santa Cruz County (Barry, 1996; U.S. Fish and Wildlife Service, 2006; Biosearch Associates, 2012). They range from the vicinity of Woodside and Crystal Springs Reservoir in eastern San Mateo County, west across the crest of the Santa Cruz Mountains to the coast, and from Mori Point near Pacifica south to Waddell Creek in northern Santa Cruz County. The San Francisco watershed supports about one-half of the entire population (Barry, 1996).

San Francisco gartersnakes occupy freshwater marshes and bordering meadows, uplands, and riparian habitat. Populations are concentrated in grassland regions where sag ponds (ponds formed where active or recent fault movement has impounded drainage) and freshwater estuaries are present or once were present (Barry 1994). Emergent and riparian vegetation—such as cattail (*Typha* spp.), spike rush (*Eleocharis* spp.), bur-reed (*Sparganium* spp.), tule (*Schoenoplectus* spp.), and willow (*Salix* spp.)—near shallow edges of fresh water (ponds, lakes, reservoirs, creeks, and drainage ditches) is crucial for foraging activities (Barry, 1994; U.S. Fish and Wildlife Service, 2006). During the

winter, San Francisco gartersnakes generally are inactive underground in rodent burrows or other cover but may emerge during warm periods. Males generally emerge first from hibernacula in early spring and promptly begin searching for mates. Female emergence follows thereafter, and pheromone trails bring the sexes together (Rossman and others, 1996). Mating aggregations also can be observed in autumn, and females can store viable sperm for many months including over the winter (Rossman and others, 1996). Females produce between 12 and 24 live young in July or August (Biosearch Associates, 2012). The home ranges of San Francisco gartersnakes have not been reported in the published literature (U.S. Fish and Wildlife Service, 2006), but individuals have been reported as far as about 200 m from aquatic habitat (Halstead and others, 2011).

About 95 percent of the San Francisco gartersnake diet consists of co-occurring amphibian species (Barry, 1996). Sierran treefrogs (*Pseudacris sierra*) are important prey species for all San Francisco gartersnake life stages, but might be particularly so for smaller snakes less than 400 mm snout-vent length (SVL). Individuals larger than 500 mm SVL also forage on threatened California red-legged frogs (*Rana draytonii*) and introduced American bullfrogs (Barry, 1994, 1996). San Francisco gartersnakes congregate in marsh and riparian habitats during the anuran breeding season in spring. They may remain throughout the summer and autumn, as long as metamorphosing anurans are present (Barry, 1994). San Francisco gartersnakes also are able to consume toxic Pacific newts (*Taricha* spp.) because of their resistance to tetrodotoxin (Brodie and others, 2002; Stebbins, 2003). San Francisco gartersnakes are sympatric with Santa Cruz gartersnakes (*Thamnophis atratus atratus*) and coast gartersnakes (*T. elegans terrestris*); coast gartersnakes usually are the most abundant among the three species (Barry, 1994). The three sympatric gartersnake species likely partition resources; it has been suggested that foraging competition does not exist between them (Barry, 1994).

San Francisco gartersnakes are sexually dimorphic for size, with females the larger sex. The SVL of most adult females is 400–800 mm; adult male SVL generally is 300–600 mm (Barry, 1994). The dorsal color pattern of San Francisco gartersnakes displays alternating longitudinal red, black, green, and blue stripes (Barry, 1996). The top of the head is red, and the belly is rich turquoise blue. San Francisco gartersnakes might intergrade with California red-sided gartersnakes (*T. s. infernalis*). The intergraded populations occur near the city of Palo Alto north to the Pulgas region near Upper Crystal Springs Reservoir (U.S. Fish and Wildlife Service, 2006).

Goals and Objectives

The primary goal of this study was to conduct an assessment of the San Francisco gartersnake response to enhancement actions at Mindego Ranch. Specific objectives included the following:

- Provide abundance estimates for the population;
- Estimate the sex ratio of the population;
- Estimate the size distribution of the population;
- Provide demographic information for the population, including per-capita recruitment, apparent survival, and population growth rates;
- Provide information on the spatial distribution of San Francisco gartersnakes at Mindego Ranch; and
- Evaluate the effects of invasive species removal and grazing on San Francisco gartersnake demography.

Study Area

The Mindego Ranch property is located in San Mateo County, California, within the historical range of San Francisco gartersnakes (Barry, 1994, 1996; fig. 1). It is a 424-ha (1,047-acre) cattle ranch that was added to the western part of the Russian Ridge Open Space Preserve by the Midpeninsula Regional Open Space District (MROSD) in 2008. San Francisco gartersnakes were first observed on the property in 1986 (Biosearch Associates, 2012). The MROSD has launched three management projects under the Mindego Ranch Use and Management Plan (Biosearch Associates, 2012) to protect and enhance habitat for sensitive wildlife species while responsibly integrating necessary land management activities and limited public access at Mindego Ranch (Ascent Environmental, 2013). The project management plans in 2012 included (1) managing habitat for San Francisco gartersnakes, (2) inventorying erosion potential on trails, and (3) implementing a conservation grazing plan (Ascent Environmental, 2013).

Prior to European contact, the land that includes Mindego Ranch was used by several Tribal groups of the Ohlone Indian cultural sphere (Biosearch Associates, 2012). The ownership of Mindego Ranch changed from Juan Medico, the first non-native settler at Mindego Ranch in 1859, to the True family in 1954; both owners had cattle that grazed grasslands on the site year-round. The True family sold the property to the Peninsula Open Space Trust in 2007. The property was subsequently transferred to MROSD in 2008 (Biosearch Associates, 2012), and grazing did not occur during 2008–2014. Mindego Ranch has four major water bodies that contain emergent and riparian vegetation with adjacent upland habitat. Prominent wetland vegetation includes spike rush, bur-reed, tule, and willow. Upland plant communities comprise mixed evergreen forest, non-native grassland, and coyote brush (*Baccharis pilularis*) scrub. Non-native grasses and forbs, as well as native shrubs, provide cover and basking spots in the upland habitat. San Francisco gartersnakes were first identified at Mindego Ranch in 1986 at Aquatic Features 2 and 3 (Biosearch Associates, 2012). They were observed near all four major water bodies between 2009 and 2012 (Biosearch Associates, 2012). Grazing resumed in 2015, when the ranch was divided into summer and winter pastures. The invasive American bullfrogs were culled from Aquatic Feature 3 in 2014 and 2015, through the joint efforts of MROSD and Biosearch Associates. The drought in 2014 caused the feature to completely dry up for the first time in many years, if not decades (Julie Andersen, Midpeninsula Regional Open Space District, written commun., April 4, 2018), eradicating larval American bullfrogs and non-native fish species including the sunfish family (Centrarchidae) and mosquitofish (*Gambusia affinis*). In 2016 and 2017, neither American bullfrog calls nor visual observations were made, suggesting a high possibility of extirpation of American bullfrogs on the property. Aquatic Feature 3 is the only permanent water body inside Mindego Ranch and is located miles away from permanent water bodies in adjacent properties.

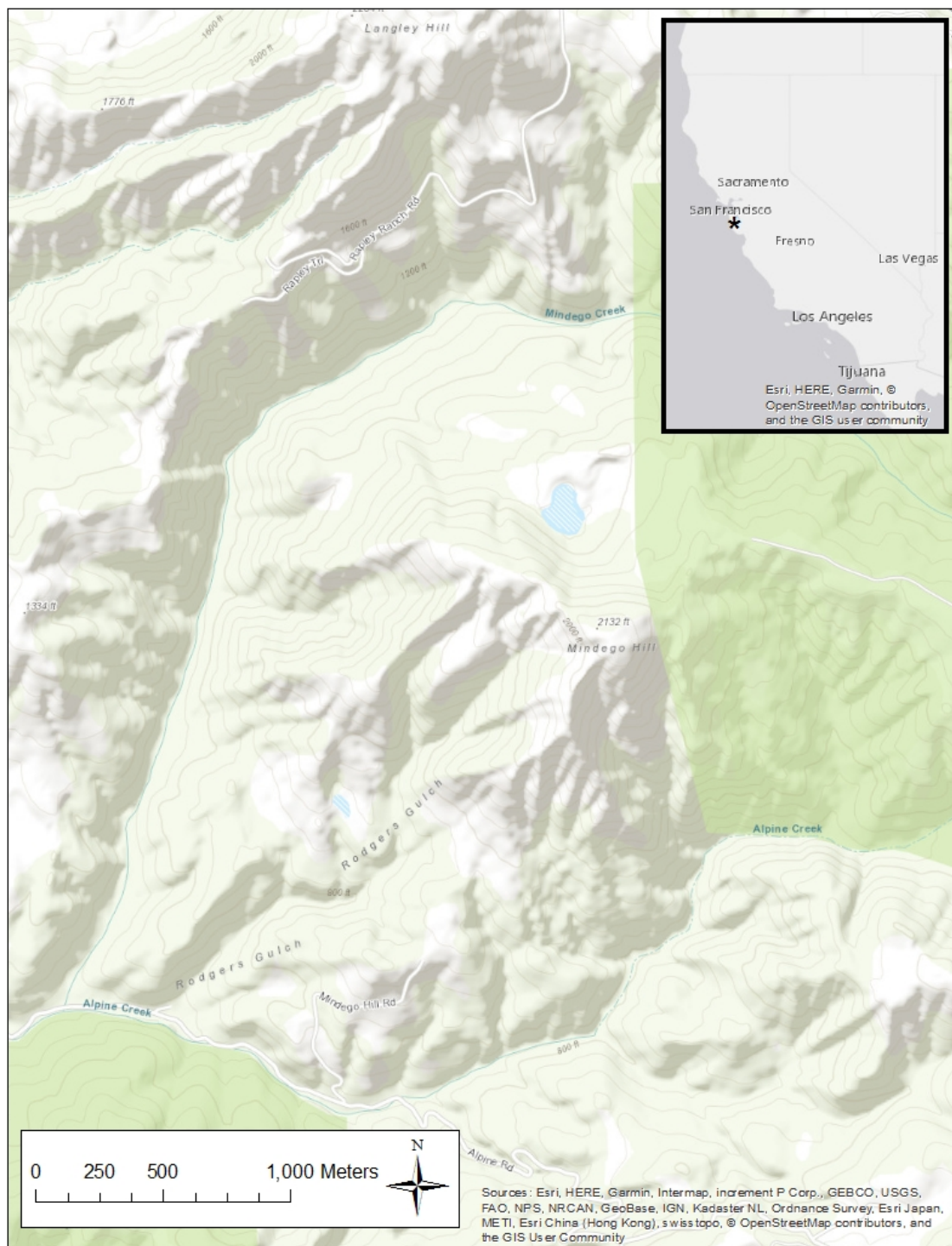


Figure 1. Schematic showing general location of Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California. The asterisk in the inset map indicates the general location of Mindego Ranch in California.

Methods

Field Methods

Capture-Mark-Recapture

We used multiple sampling methods to detect and capture San Francisco gartersnakes. We trapped for San Francisco gartersnakes using drift fence and funnel trap arrays and cover objects (Halstead and others, 2011) near the four major water bodies in Mindego Ranch. We located trap arrays within randomly selected 50×50 -m blocks, stratified by habitat, and within 100 m (mean = 60 m) of the four major water bodies. The number of arrays associated with each water body was scaled to water body area: two arrays were associated with Aquatic Feature 4, four arrays were associated with Aquatic Feature 3, three arrays were associated with Aquatic Feature 1, and three arrays were associated with Aquatic Feature 2. We located trap arrays along ecotones (transition areas between two different habitat types) within blocks when possible to improve snake capture rates based on past observations. Six trap arrays were located in unforested upland habitat, five trap arrays were located in forested or riparian habitat, and one trap array was located near marsh habitat. We constructed each drift fence from 3.2-mm Masonite® strips placed on edge (30-cm tall by 15-m long), and placed two single-ended funnel traps constructed of 3.2-mm hardware cloth secured around a wooden frame on both ends of the drift fence, one on each side, for a total of four traps per array (Halstead and others, 2011). When the traps were not in use, we closed them by plugging the opening with a 5.1-cm Styrofoam™ ball secured by a small nail pierced through the hardware cloth. Beginning in 2015, we also deployed 12 transects of 10 artificial cover objects (1.6-cm plywood cut into 0.8×1.2 -m pieces and corrugated sheet metal cut into 0.6×1.2 -m pieces) within randomly selected 50×50 -m blocks, stratified by habitat, and within 200 m of the four major water bodies. As for trap arrays, we placed cover objects along ecotones whenever possible.

We exploited seasonal and thermal activity patterns of San Francisco gartersnakes to maximize capture probabilities for demographic study. We opened traps from the beginning of April through the end of May each year, when snakes have emerged from brumation and are foraging and searching for mates. We opened traps for a minimum of 45 consecutive days each year. We checked traps twice daily while open and used moistened sponges to avoid desiccation or thermal stress of captured individuals. We checked cover objects during the early morning or on cold days, when snakes are more likely to take cover under objects with higher heat conductivity than the surrounding environment (Engelstoft and Ovaska, 2000). We also captured San Francisco gartersnakes that were opportunistically encountered by hand, and we used a handheld Global Positioning System to mark the location of each capture. For each day of sampling, we monitored environmental conditions relevant to San Francisco gartersnake behavior. In particular, we measured air temperatures, sky condition (cloud cover or haze), and rain or fog within the preceding 24 hours.

We examined the sex of, measured, and uniquely marked each captured San Francisco gartersnake to assess the demography of the San Francisco gartersnake population at Mindego Ranch. We measured SVL and tail length of each individual to the nearest millimeter, and weighed each individual to the nearest gram. We determined the sex of each individual by probing the cloaca to detect the presence or absence of hemipenes (Fitch, 1960). We did not probe small individuals weighing less than 15 g to prevent injury to the snake; extra care also was given to these small individuals when uniquely marking them. After examination, each individual that showed no sign of previous capture was given a unique brand on its ventral scutes (fig. 2; Winne and others, 2006). We processed most individuals in the field within minutes of their capture. Each individual San Francisco gartersnake was released at its location of capture immediately after processing.

We also measured, sexed, and uniquely marked other snake species present at Mindego Ranch, including coast gartersnakes, Santa Cruz gartersnakes, Pacific gophersnakes (*Pituophis catenifer catenifer*), western yellow-bellied racers (*Coluber mormon*), northern rubber boas (*Charina bottae*), Pacific ring-necked snakes (*Diadophis punctatus amabilis*), and sharp-tailed snakes (*Contia tenuis*). We neither collected nor handled northern Pacific rattlesnakes (*Crotalus oreganus oreganus*). To obtain a measure of the local relative abundance and diversity of potential terrestrial prey, we also recorded the vertebrate contents of all traps and then removed them. We did not record invertebrate trap contents.



Figure 2. Photographs showing (A) application of a brand to a giant gartersnake (*Thamnophis gigas*) with a medical cautery device, and (B) the appearance of a properly completed brand (indicated by white arrows). Photograph by Shannon Skalos, U.S. Geological Survey, Colusa National Wildlife Refuge, May 2013.

Habitat Characterization

We characterized the habitats sampled by trap arrays to examine the influence of habitat on occurrence and abundance of San Francisco gartersnakes. We recorded the Universal Transverse Mercator coordinates of all trap and cover object locations and conducted vegetation and habitat surveys at random points associated with each trap array in April. We used uniform random bearings (1° – 360°) and distances (maximum = 25 m) to select 12 random survey points per trap array. Three random points were allocated to each quadrant to ensure adequate spatial representation of the vegetation around each array. A total of 144 quadrats were assessed for habitat characteristics each year. We visually estimated the percent cover of habitat types (open water, submerged vegetation, emergent vegetation, terrestrial herbaceous vegetation, woody vegetation, litter, rock, or bare ground) and vegetative composition (species or higher taxonomic category) within a circle of 1-m diameter centered on the random point.

Amphibian Surveys

We supplemented San Francisco gartersnake surveys with surveys targeting their amphibian prey to estimate prey availability. We conducted nocturnal eye shine surveys for California red-legged frogs and American bullfrogs between January and April, focusing our survey efforts on the perimeters of Aquatic Features 2 and 3. Survey dates were entirely dependent on daily weather conditions; nights with rain or heavy fog were avoided because of the visual obstruction they caused. We surveyed Aquatic Feature 3 three times. Two observers started from an arbitrary location along the perimeter of the feature and used handheld spotlights and binoculars to shine on the opposite shore and to count the number of reflected eye shines (Corben and Fellers, 2001; Fellers and Kleeman, 2006). The observers then relocated to the opposite shore and repeated the same procedure. To account for detectability, we used a dependent double-observer technique (Grant and others, 2005), in which the first observer pointed to each eye shine and counted out to the second observer, who recorded what the first observer reported but also separately recorded any additional eye shines that the first observer missed (Grant and others, 2005); halfway through the survey, the first and second observers switched roles. We distinguished California red-legged frogs from American bullfrogs by various methods. American bullfrogs have distinctively larger tympana (eardrums) than California red-legged frogs. When observed under spotlights and binoculars, American bullfrogs are dark forest green with dark brown spots on smooth skin, whereas California red-legged frogs are dark brown and have two distinctive dorsolateral folds.

Analytical Methods

Sex Ratios and Size Distributions

We calculated sex ratios and size distributions of San Francisco gartersnakes at Mindego Ranch using standard statistical models, which do not account for potential biases in capture probabilities. We estimated naïve sex ratios with a binomial model using an uninformative prior (*uniform(minimum = 0, maximum = 1)* for the probability of being male). Because the binomial model is based on sampling with replacement, we used the total number of captures of each sex, rather than the number of individuals of each sex, as input for the model (Skalski and others, 2005). To estimate the size distribution of San Francisco gartersnakes, we fit a lognormal model, which restricts values to be positive and allows for the positive skewness often observed in snake size distributions. We accounted for sexual size dimorphism (Barry, 1994) by estimating the mean SVL and mass of males and females independently, and calculated the difference between means as a derived parameter to examine the difference in size between the sexes. We used uninformative priors (*uniform(0, 1000)* for means and standard deviations) for this analysis. We conducted a Bayesian analysis of the sex ratio

and sexual size dimorphism models using Markov chain Monte Carlo (MCMC) techniques. Models were run on five independent chains of 100,000 iterations each after a burn-in of 10,000; each chain was thinned by a factor of five, so inference was based on 100,000 iterations from the stationary posterior distribution. We examined potential scale-reduction factors (Gelman and Rubin, 1992) to assess convergence and found no evidence of lack of convergence ($R\text{-hat} < 1.1$). We analyzed these models by calling OpenBUGS version 3.2.3 (Thomas and others, 2006) from R version 3.1.0 (R Core Team, 2015) using the R packages R2OpenBUGS (Sturtz and others, 2005) and hdi (Dezeure and others, 2014). Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

Abundance and Demographic Rates

We estimated the abundance and demographic rates of San Francisco gartersnakes at Mindego Ranch using capture-mark-recapture (CMR) techniques. We used all captures during the spring sampling period (April and May) for these analyses. We estimated annual abundances using closed population models, which assume that the population is closed to additions through birth and immigration and to removals through death and emigration throughout the survey period. Open population models relax this assumption, and we used open population models to estimate survival, recruitment, and population growth rate between years, as well as annual abundance.

Closed Population Models

We estimated abundance of San Francisco gartersnakes at Mindego Ranch in each year. Parameters of the closed model were estimated using Bayesian analysis of CMR data with data augmentation (Royle and others, 2007; Royle and Dorazio, 2008; Royle, 2009). Data augmentation is an approach to CMR analysis in which a large number of all zero capture histories is appended to the observed capture histories. The abundance estimation problem then seeks to answer the question: How many undetected individuals were actually a part of the population but not observed? This approach is much more flexible than other approaches to estimation of abundance and allows a unified framework for analysis of detection-nondetection and CMR data (Royle and Dorazio, 2008).

The closed population model included effects of sex, SVL, air temperature, date, an ephemeral behavioral response to capture (capture on day $t-1$ affected capture on day t , but effects did not persist), and unexplained random temporal variation on daily individual capture probabilities. The model did not contain any interactions among variables. We standardized all continuous variables to improve behavior of the MCMC algorithm and to allow direct comparison of model coefficients. We calculated the posterior probability of each subset of the full model using indicator variables on model parameters (Kuo and Mallick, 1998; Royle and Dorazio, 2008). We augmented the capture histories of trapped individuals with 500 all-zero capture histories (pseudo-individuals). Five hundred pseudo-individuals were deemed adequate because the most of the posterior density for abundance was much less than 500. We used uninformative priors for all parameters: *uniform*(0,1) for probabilities, *normal*(mean = 0, standard deviation = 3.16) for regression coefficients, *uniform*(0,10) for standard deviations, and *binomial*($n = 1$, $p = 0.5$) for indicator variables. Models were run on five independent chains of 100,000 iterations each after a burn-in of 50,000; each chain was thinned by a factor of five so that inference was based on a sample of 100,000 iterations from the stationary posterior distribution. We examined potential scale-reduction factors (Gelman and Rubin, 1992) to assess convergence and found no evidence of lack of convergence ($R\text{-hat} < 1.1$). We analyzed the model by calling Just Another Gibbs Sampler (JAGS) version 3.4.0 (Plummer, 2014) from R version 3.2.1 (R Core Team, 2015) using the R package jagsUI (Kellner, 2016). Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

Open Population Models

To estimate demographic rates, we fit Jolly-Seber models (Jolly, 1965; Seber, 1965; Williams and others, 2002) for open populations to data from all 4 years of sampling (2014–17) at Mindego Ranch. Open population models are more complex than closed population models because in addition to abundance, these models also estimate demographic rates, including recruitment, apparent survival, and population growth rates. Recruitment is the process by which new individuals are added to the population and includes birth and immigration. Our model included independent recruitment probabilities in each year, and we express results as per-capita recruitment—the number of new individuals in year t per individual alive and in the population in year $t - 1$. Apparent survival is the process by which individuals leave the population, and includes mortality and permanent emigration. We allowed estimates of apparent survival to vary among years as an annual random effect; similarly, we allowed daily capture probability to vary among years as an annual random effect, but assumed that it was constant within years. We also reported the instantaneous per-capita growth rate (r), rather than the geometric growth rate (λ) usually used for populations that reproduce in discrete time, because of the interpretability of r (it is symmetric about 0, rather than asymmetric about 1). Probabilities are provided for benchmarks of population change (10-percent increase, 10-percent decrease, and stability [less than 10-percent change in either direction]). Like the closed population analysis, the Jolly-Seber analysis used uninformative priors, including *Dirichlet*(1,1,1,1) priors for entrance probabilities and *beta*(1,1) priors on mean annual daily capture and annual survival probabilities. Annual daily capture and annual survival probabilities were allowed to vary from the mean as a random effect distributed on the logit-scale as *normal*(0, σ_p) and *normal*(0, σ_ϕ), with σ_p and σ_ϕ given *half-Cauchy*(1) priors. We ran the model on five independent chains of 200,000 iterations each, after a burn-in of 20,000 iterations. We thinned the output by a factor of 10, so that inference was based on a sample of 100,000 iterations from the stationary posterior distribution. We examined potential scale-reduction factors (Gelman and Rubin, 1992) to assess convergence and found no evidence of lack of convergence (R-hat < 1.1). We called JAGS version 3.4.0 (Plummer, 2014) from R version 3.2.1 (R Core Team, 2015) using the package *runjags* (Denwood, 2016) to run this analysis. Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

Spatial Distribution

We examined the spatial distribution of San Francisco gartersnakes at Mindego Ranch with single-season (static) occupancy models (MacKenzie and others, 2002, 2005, 2006; Tyre and others, 2003) and binomial mixture models (Kéry and others, 2005; Kéry, 2008, 2010; Kéry and Schaub, 2011), and explored changes in the distribution of snakes using dynamic occupancy models (MacKenzie and others, 2006; Royle and Kéry, 2007; Kéry and Schaub, 2011). Each of these models uses repeated surveys at multiple sites (in this case, trap arrays) to estimate detection probabilities and account for false absences that occur when a species is present at a site (or array), but we fail to detect it. Similar to closed population models, static occupancy models assume that sites are closed to colonization and extirpation, and binomial mixture models assume that sites are closed to changes in abundance during the survey period. We, therefore, estimated trap array occurrence and relative abundance of San Francisco gartersnakes independently for each year with these models. Dynamic occupancy models are similar to open population models in that they relax the closure assumption and allow the estimation of changes in occupancy through the processes of colonization and extirpation over time.

Static Occupancy Models

We analyzed the annual probability of occurrence (ψ) of San Francisco gartersnakes in trap arrays at Mindego Ranch using static occupancy models independently for each year. Static occupancy models use the pattern of daily detections and non-detections at each trap array to estimate detection probabilities, and from these data, to correct estimates of occurrence for false absences. For the single-season occupancy analysis, we treated each trap array as a site, and each trapping day as a sample. We evaluated evidence for the effects of air temperature, rain, and unexplained temporal and spatial heterogeneity on detection probabilities, and the effects of habitat diversity, distance from wetland, and unexplained site heterogeneity on ψ using indicator variables on model coefficients (Kuo and Mallick, 1998; Royle and Dorazio, 2008). Habitat diversity was calculated as the Shannon (or Shannon-Weaver) index ($H' = -\sum_{i=1}^R prop_i \ln prop_i$; Shannon and Weaver, 1948), where $prop_i$ is the proportion of habitat i in the array, and R is the total number of habitat categories. We used uninformative priors for all model coefficients. We gave all probabilities, including mean detection and occupancy probabilities *uniform*(0,1) priors, all logit-scale standard deviations *half-Cauchy* priors specified as $t(0,1,1)$ truncated at a lower limit of 0, model coefficients hierarchical $t(0,\sigma_{coef},1)$ priors (Kruschke, 2015), and indicator variables *binomial*(1,0.5) priors. We ran the model on five independent chains of 200,000 iterations each after a burn-in of 20,000 iterations. We thinned the output by a factor of 10, so that inference was based on a sample of 100,000 iterations from the stationary posterior distribution. We examined potential scale-reduction factors (Gelman and Rubin, 1992) to assess convergence and found no evidence of lack of convergence (R-hat <1.1). We called JAGS version 3.4.0 (Plummer, 2014) from R version 3.2.1 (R Core Team, 2015) using the package jagsUI (Kellner, 2016) to run this analysis. Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

Binomial Mixture Models

In contrast to single-season occupancy models, binomial mixture models account for differences in abundance among sites. Binomial mixture models do not require marked individuals, but instead require repeated counts at multiple sites. From the repeated counts, detection probability can be estimated and imperfect detection can be accounted for in the analysis. Because the models do not require marked individuals and assume equal capture probabilities among individuals, they cannot estimate true abundance at each trap array (Barker and others, 2017); therefore, we reported the proportional abundance of San Francisco gartersnakes at each array to describe their spatial distribution. We treated each trap array as a site, and pooled observations into multiple 5- or 6-day periods. As for single-season occupancy, we evaluated evidence for the effects of air temperature, rain, and unexplained temporal heterogeneity on detection probabilities, and the effects of habitat diversity, distance from wetland, and unexplained site heterogeneity on abundance using indicator variables (Kuo and Mallick, 1998; Royle and Dorazio, 2008). We used uninformative priors for all model parameters. We gave all probabilities, including mean detection and occupancy probabilities, *uniform*(0,1) priors, all logit-scale standard deviations *half-Cauchy* priors specified as $t(0,1,1)$ truncated at a lower limit of 0, model coefficients hierarchical $t(0,\sigma_{coef},1)$ priors (Kruschke, 2015), and indicator variables *binomial*(1,0.5) priors. We ran the model on five independent chains of 200,000 iterations each after a burn-in of 20,000 iterations. We thinned the output by a factor of 10, so that inference was based on a sample of 100,000 iterations from the stationary posterior distribution. We examined potential scale-reduction factors (Gelman and Rubin, 1992) to assess convergence and found no evidence of lack of convergence (R-hat <1.1). We called JAGS version 3.4.0 (Plummer, 2014) from R version 3.2.1 (R Core Team, 2015) using the package jagsUI (Kellner, 2016) to run this analysis. Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

Dynamic Occupancy Models

In addition to the single-season occupancy models, we used dynamic occupancy models (MacKenzie and others, 2006; Royle and Kéry, 2007; Kéry and Schaub, 2011) to examine how the distribution of San Francisco gartersnakes at Mindego Ranch changed over time (Royle and Dorazio, 2008). In contrast to static occupancy models, dynamic occupancy models allow for changes in occupancy and model the probability that trap arrays occupied at time t remain occupied at $t+1$ (persistence, which equals $1 - \text{extirpation}$), or that those unoccupied at time t are occupied at time $t+1$ (colonization). The model allowed for the effects of site variables (habitat diversity, distance to the closest water body, unexplained site heterogeneity, and annual heterogeneity) on colonization and persistence probabilities. We evaluated evidence for the effects of air temperature, Julian date, and rain on detection probabilities. We calculated the posterior probability of each subset of the full model using indicator variables on model parameters (Kuo and Mallick, 1998; Royle and Dorazio, 2008). We used uninformative priors for all model coefficients. We gave all probabilities (including mean detection and occupancy probabilities and model coefficients) $normal(0, 1.65)$ priors, all logit-scale standard deviations $uniform(0, 10)$ priors, and indicator variables $binomial(1, 0.5)$ priors. We ran the model on five independent chains of 20,000 iterations each after a burn-in of 2,000 iterations. We thinned the output by a factor of 5, so that inference was based on a sample of 20,000 iterations from the stationary posterior distribution. We examined potential scale-reduction factors (Gelman and Rubin, 1992) to assess convergence and found no evidence of lack of convergence ($R\text{-hat} < 1.1$). We called JAGS version 3.4.0 (Plummer, 2014) from R version 3.2.1 (R Core Team, 2015) using the package jagsUI (Kellner, 2016) to run this analysis. Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

Effect of Non-Native Aquatic Vertebrate Removal on Survival and Recruitment

We examined the effects of American bullfrog abundance on recruitment and survival of San Francisco gartersnakes using Pradel temporal symmetry models (Pradel, 1996). These models assess capture histories for each San Francisco gartersnake in “forward” and “reverse” directions; individuals marked and released at time t that are recaptured at time $t+k$ must have survived at least k years (survival), and individuals that are captured at time t and had earlier been captured at time $t-k$ must have entered the population at least k years ago (seniority). We used a Bayesian analysis of the survival (ϕ) and seniority (γ) parameterization of the model, and calculated population growth rate ($\lambda_i = \frac{\phi_i}{\gamma_{i+1}}$), recruitment ($f_i = \phi_i \left(\frac{1 - \gamma_{i+1}}{\gamma_{i+1}} \right)$) and proportion of population composed of new recruits ($1 - \gamma$) as derived parameters (Tenan and others, 2014; Cooch and White, 2017). We modeled the effect of bullfrog abundance on survival and recruitment using logistic regression for both parameters, and allowed capture probability (p) to vary annually using a logit-normal random effect. We specified all priors to be uninformative, with all mean probabilities having $beta(1, 1)$ priors, logit-scale coefficients having $normal(0, 1.6)$ priors, and the standard deviation of the logit-scale random variation in p having a *half-Cauchy*(1) prior. To improve convergence, we standardized bullfrog abundance prior to analysis. We ran the model on five independent chains of 200,000 iterations each after a burn-in of 20,000 iterations. We thinned the output by a factor of 10, so that inference was based on a sample of 100,000 iterations from the stationary posterior distribution. We called JAGS version 3.4.0 (Plummer, 2014) from R version 3.2.1 (R Core Team, 2015) using the package jagsUI (Kellner, 2016) to run this analysis. Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

Amphibian Abundance

We estimated abundance of California red-legged frogs, American bullfrogs, and Sierran treefrogs in 2014 and 2015. We used hierarchical binomial and Poisson models to estimate abundance of (1) Sierran treefrog egg masses and (2) adult and recently metamorphosed California red-legged frogs and American bullfrogs from removal counts (Williams and others, 2002) based on dependent double-observer surveys (Grant and others, 2005), but we did not quantify the abundance of larval anurans. Dependent double-observer methods account for imperfect detection of animals by surveyors, due to surveyor errors or environmental factors (Grant and others, 2005), when a population is sampled on separate occasions and the animals observed on each occasion are “counted out” (removed) from the population. We used a binomial distribution for detection probability, conditioned on the number of individuals available to be detected. We allowed each observer to have a different baseline detection probability, and in some cases allowed as many as two covariates, including vegetation density or environmental conditions. Covariates were assumed to have the same effect on detection probabilities for both observers. When estimating the number of Sierran treefrogs from the abundance of egg masses, we assumed three clutches per female (Perrill and Daniel, 1983) and a 1:1 sex ratio (Oplinger, 1966). We gave all probabilities, including the mean intercepts and coefficients for each variable, $normal(0, 1.65)$ priors. We ran the model on five independent chains of 200,000 iterations each after a burn-in of 9,000 iterations. We thinned the output by a factor of 10, so that inference was based on a sample of 100,000 iterations from the stationary posterior distribution. We examined potential scale-reduction factors (Gelman and Rubin, 1992) to assess convergence and found no evidence of lack of convergence ($R\text{-hat} < 1.1$). We analyzed the model by calling JAGS version 3.4.0 (Plummer, 2014) from R version 3.2.1 (R Core Team, 2015) using the R package *runjags* (Denwood, 2016). Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

In addition to the estimated abundance from egg mass counts and eye shine surveys, we used an open population N-mixture model (Dail and Madsen, 2011) to estimate the abundance of Sierran treefrogs captured as funnel trap bycatch during the sampling period. An assumption inherent in a conventional N-mixture model is that populations at each array are assumed closed to additions and removals throughout the survey period. Because metamorphosed Sierran treefrogs were recruited into the population between April and May, we fit an open population N-mixture model, which does not require the assumption that population is closed (Dail and Madsen, 2011). We pooled the trap bycatch every 9 days, rather than every 5–6 days as for snake N-mixture models, because the number of captures was very sparse when pooling only 5 or 6 days. We modeled abundance at each pooled period as a function of previous abundance and covariates, including percentage of rainy days, air temperature, Julian date, and array-specific heterogeneity. We used Julian date and array-specific heterogeneity as covariates that affected detection probability. We used uninformative priors for all parameters— $uniform(0, 10)$ for the standard deviations, $uniform(0, 100)$ for mean abundance, and $normal(0, 3.16)$ for mean intercepts and coefficients for each variable. We ran the model on three independent chains of 10 million iterations each after a burn-in of 9,000 iterations. We thinned the output by a factor of 10, so that inference was based on a sample of 3 million iterations from the stationary posterior distribution. We examined potential scale-reduction factors (Gelman and Rubin, 1992) to assess convergence and found no evidence of lack of convergence ($R\text{-hat} < 1.1$). We analyzed the model by calling JAGS version 3.4.0 (Plummer, 2014) from R version 3.2.1 (R Core Team, 2015) using the R package *runjags* (Denwood, 2016). All models for estimating amphibian abundance did not contain any interactions among variables. Posterior distributions were summarized by the posterior mode (95-percent highest posterior density interval), unless otherwise indicated.

Results

Captures

Overall, we observed 198 individual San Francisco gartersnakes (113 males, 82 females, 3 unknown) 345 times by all methods at Mindego Ranch between April and May, 2014–17 (table 1). Habitats sampled by trap arrays varied from one another, but habitats at individual arrays were relatively stable during 2014–17 (tables 2–5).

Table 1. San Francisco gartersnake (*Thamnophis sirtalis tetrataenia*) capture dates, sexes, sizes, and locations at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[**Abbreviations:** ID, unique numeric brand applied to ventral scales; SVL, snout-vent length; g, gram; mm, millimeter; NA, not applicable because snake was not captured, or was recently captured and measured]

ID	Date	Sex	SVL (mm)	Mass (g)	Method
NA	18-May-14	NA	NA	NA	Sighting
999	5-Apr-14	Female	647	108	Hand capture
1000	2-May-16	Male	550	70	Funnel trap
1000	9-Apr-14	Male	470	51	Funnel trap
1000	11-Apr-14	Male	NA	NA	Funnel trap
1001	10-May-16	Female	670	190	Cover object
1001	8-Apr-14	Female	456	37	Hand capture
1001	13-May-14	Female	510	45	Funnel trap
1002	10-Apr-14	Female	225	5	Funnel trap
1003	4-Apr-15	Female	625	180	Funnel trap
1003	2-Apr-16	Female	700	200	Cover object
1003	5-Apr-16	Female	700	NA	Cover object
1003	8-Apr-14	Female	625	111	Funnel trap
1004	3-May-15	Female	620	134	Funnel trap
1004	10-Apr-14	Female	596	76	Funnel trap
1004	13-Apr-14	Female	NA	NA	Funnel trap
1006	3-Apr-15	Female	475	41	Funnel trap
1006	11-Apr-14	Female	310	11	Funnel trap
1007	8-Apr-14	Male	438	38	Funnel trap
1008	11-Apr-14	Female	530	94	Funnel trap
1009	2-May-16	Female	615	150	Funnel trap
1009	8-Apr-14	Female	440	42	Hand capture
1010	11-Apr-14	Female	543	90	Funnel trap
1011	24-Apr-15	Male	600	94	Hand capture
1011	12-Apr-14	Male	580	87	Funnel trap
1011	2-May-14	Male	NA	NA	Funnel trap
1012	18-Apr-16	Male	535	74	Funnel trap
1012	19-Apr-16	Male	535	NA	Funnel trap
1012	13-Apr-14	Male	475	45	Funnel trap
1013	14-Apr-14	Male	410	36	Funnel trap
1013	29-Apr-14	Male	NA	NA	Funnel trap
1014	2-May-16	Male	610	80	Funnel trap
1014	16-Apr-14	Male	585	104	Funnel trap
1015	16-Apr-14	Male	500	46	Funnel trap
1015	18-Apr-14	Male	NA	NA	Funnel trap
1016	18-Apr-14	Female	370	23	Funnel trap
1017	22-Apr-14	Male	510	41	Funnel trap
1018	28-Apr-14	Female	722	170	Funnel trap
1018	2-May-14	Female	NA	NA	Funnel trap
1019	29-Apr-14	Male	590	71	Funnel trap
1020	2-May-14	Male	480	40	Hand capture
1021	2-Apr-15	Male	545	71	Hand capture

ID	Date	Sex	SVL (mm)	Mass (g)	Method
1021	8-Apr-15	Male	NA	NA	Hand capture
1021	3-May-14	Male	530	62	Funnel trap
1022	3-May-14	Female	620	144	Funnel trap
1023	2-May-16	Male	540	70	Funnel trap
1023	3-May-16	Male	540	NA	Funnel trap
1023	4-May-16	Male	540	NA	Funnel trap
1023	3-May-14	Male	410	30	Funnel trap
1024	8-May-14	Female	530	95	Cover object
1025	8-May-14	Male	540	71	Trap array
1025	20-May-14	Male	NA	NA	Trap array
1026	9-May-14	Female	725	156	Hand capture
1026	14-May-14	Female	NA	NA	Trap array
1027	10-May-14	Male	310	10	Hand capture
1028	14-May-14	Female	635	91	Trap array
1029	27-Apr-15	Female	555	104	Cover object
1029	15-May-14	Female	360	23	Hand capture
1030	16-May-14	Female	815	241	Trap array
1031	18-May-14	Male	310	11	Hand capture
1032	19-May-14	Female	305	18	Hand capture
1033	10-Apr-15	Male	430	32	Trap array
1033	18-Apr-16	Male	500	67	Funnel trap
1033	21-May-14	Male	320	19	Trap array
1034	24-Apr-15	Female	700	204	Hand capture
1034	15-May-16	Female	730	250	Hand capture
1034	22-May-16	Female	730	NA	Funnel trap
1034	21-May-14	Female	660	146	Trap array
1035	21-May-14	Unknown	247	15	Trap array
1036	12-Apr-15	Male	510	47	Trap array
1036	12-May-15	Male	NA	NA	Hand capture
1036	10-May-16	Male	505	55	Funnel trap
1037a	12-Apr-15	Male	455	40	Trap array
1037a	10-May-15	Male	480	63	Trap array
1037a	13-May-16	Male	550	60	Funnel trap
1037a	30-Apr-17	Male	540	61	Funnel trap
1037a	4-May-17	Male	NA	NA	Funnel trap
1037a	17-May-17	Male	570	60	Funnel trap
1037b	15-Apr-15	Male	445	35	Trap array
1038b	10-Apr-15	Female	650	165	Hand capture
1039	27-Apr-15	Male	500	64	Trap array
1039	2-May-16	Male	555	61	Funnel trap
1042	23-Apr-16	Male	540	75	Funnel trap
1043	4-Apr-15	Female	585	90	Trap array
1043	14-Apr-16	Female	610	140	Funnel trap
1044	10-Apr-15	Unknown	350	17	Trap array
1045	10-Apr-15	Male	530	62	Trap array
1045	11-Apr-15	Male	NA	NA	Trap array
1046	11-Apr-15	Female	485	51	Trap array
1047	11-Apr-15	Male	580	73	Trap array
1047	29-Apr-15	Male	NA	NA	Trap array
1048	12-Apr-15	Male	520	46	Trap array
1048	12-Apr-15	Male	NA	NA	Trap array
1048	28-Apr-15	Male	NA	NA	Trap array
1048	21-Apr-17	Male	545	58	Funnel trap
1048	28-Apr-17	Male	NA	NA	Funnel trap
1048	18-May-17	Male	NA	NA	Funnel trap
1049	12-Apr-15	Female	300	15	Trap array
1050	13-Apr-15	Male	460	40	Trap array
1050	15-Apr-15	Male	NA	NA	Trap array
1050	24-Apr-15	Male	NA	NA	Hand capture

ID	Date	Sex	SVL (mm)	Mass (g)	Method
1050	5-Apr-16	Male	520	55	Funnel trap
1051	16-Apr-15	Male	485	45	Trap array
1051	29-Apr-16	Male	530	63	Funnel trap
1052	19-Apr-15	Male	550	81	Trap array
1052	2-Apr-16	Male	600	85	Cover object
1052	5-Apr-16	Male	600	NA	Cover object
1052	10-Apr-17	Male	585	86	Funnel trap
1053	20-Apr-15	Female	735	201	Hand capture
1054	20-Apr-15	Female	570	114	Hand capture
1054	29-Apr-16	Female	600	150	Cover object
1054	18-May-16	Female	600	130	Funnel trap
1055	24-Apr-15	Female	630	124	Hand capture
1056	24-Apr-15	Male	411	44	Hand capture
1057	24-Apr-15	Male	350	24	Hand capture
1058	24-Apr-15	Female	655	184	Hand capture
1059	28-Apr-15	Male	480	66	Trap array
1059	30-Apr-15	Male	NA	NA	Trap array
1060	28-Apr-15	Male	475	54	Trap array
1061	30-Apr-15	Female	605	133	Cover object
1062	2-May-15	Male	505	74	Trap array
1063	5-May-15	Female	580	126	Trap array
1063	7-May-15	Female	NA	NA	Trap array
1064	8-May-15	Male	345	34	Trap array
1064	2-May-16	Male	480	49	Funnel trap
1064	3-May-16	Male	480	NA	Funnel trap
1065	11-May-15	Female	500	63	Cover object
1066	12-May-15	Female	680	164	Hand capture
1067	30-Apr-16	Male	550	73	Funnel trap
1067	1-May-16	Male	550	70	Funnel trap
1067	20-Apr-17	Male	565	61	Funnel trap
1072	7-Apr-16	Female	550	73	Funnel trap
1072	8-Apr-16	Female	550	NA	Funnel trap
1072	1-May-16	Female	560	85	Funnel trap
1076	13-May-16	Female	500	65	Funnel trap
1077	3-Apr-16	Male	450	42	Funnel trap
1077	10-May-16	Male	490	55	Funnel trap
1077	16-May-16	Male	490	NA	Funnel trap
1078	4-Apr-16	Female	420	35	Funnel trap
1078	19-Apr-16	Female	420	35	Funnel trap
1079	4-Apr-16	Male	450	47	Funnel trap
1080	5-Apr-16	Male	480	56	Funnel trap
1081	5-Apr-16	Male	445	42	Funnel trap
1081	30-Apr-17	Male	520	40	Funnel trap
1082	5-Apr-16	Unknown	390	35	Hand capture
1083	5-Apr-16	Female	485	54	Funnel trap
1083	25-Apr-17	Female	600	140	Funnel trap
1083	15-May-17	Female	607	133	Funnel trap
1084	5-Apr-16	Male	480	58	Hand capture
1085	5-Apr-16	Female	275	30	Funnel trap
1086	6-Apr-16	Male	490	52	Funnel trap
1087	6-Apr-16	Male	390	37	Funnel trap
1087	13-Apr-16	Male	NA	NA	Funnel trap
1088	7-Apr-16	Male	470	60	Cover object
1088	1-May-16	Male	NA	NA	Funnel trap
1089	7-Apr-16	Male	410	40	Funnel trap
1090	13-Apr-16	Male	450	39	Funnel trap
1090	18-Apr-16	Male	NA	NA	Funnel trap
1091	13-Apr-16	Female	490	60	Funnel trap
1092	13-Apr-16	Male	495	60	Funnel trap

ID	Date	Sex	SVL (mm)	Mass (g)	Method
1093	14-Apr-16	Female	380	32	Funnel trap
1093	15-Apr-16	Female	NA	NA	Funnel trap
1094	15-Apr-16	Male	560	88	Funnel trap
1094	16-Apr-16	Male	NA	NA	Funnel trap
1094	12-May-16	Male	NA	NA	Funnel trap
1094	18-May-16	Male	NA	NA	Funnel trap
1095	15-Apr-16	Female	485	65	Funnel trap
1096	16-Apr-16	Male	530	66	Cover object
1096	1-May-16	Male	NA	NA	Funnel trap
1096	2-May-16	Male	NA	NA	Funnel trap
1096	16-May-16	Male	500	60	Funnel trap
1096	18-May-17	Male	550	61	Funnel trap
1097	16-Apr-16	Female	435	40	Funnel trap
1097	29-Apr-17	Female	540	108	Funnel trap
1097	4-May-17	Female	595	120	Funnel trap
1098	17-Apr-16	Male	370	30	Funnel trap
1099	17-Apr-16	Male	550	80	Funnel trap
1099	3-Apr-17	Male	590	60	Funnel trap
1100a	17-Apr-16	Female	485	40	Funnel trap
1100b	21-Apr-17	Male	490	42	Funnel trap
1101	18-Apr-16	Female	315	34	Funnel trap
1102	18-Apr-16	Male	510	60	Funnel trap
1102	2-May-16	Male	NA	NA	Funnel trap
1102	15-May-17	Male	520	53	Funnel trap
1103	19-Apr-16	Male	365	31	Hand capture
1104	19-Apr-16	Female	420	35	Funnel trap
1104	10-May-16	Female	NA	NA	Funnel trap
1105	19-Apr-16	Male	490	49	Funnel trap
1105	28-Apr-17	Male	530	60	Funnel trap
1105	29-Apr-17	Male	NA	NA	Funnel trap
1105	30-Apr-17	Male	NA	NA	Funnel trap
1106	25-May-16	Female	490	75	Funnel trap
1107	29-Apr-16	Female	570	130	Cover object
1108	30-Apr-16	Female	500	63	Funnel trap
1109	1-May-16	Female	500	60	Funnel trap
1110	30-Apr-16	Male	480	45	Funnel trap
1110	3-May-16	Male	NA	NA	Funnel trap
1110	4-May-16	Male	NA	NA	Funnel trap
1111	3-May-16	Female	605	150	Funnel trap
1111	3-May-17	Female	640	170	Funnel trap
1112	3-May-16	Male	405	32	Funnel trap
1113	3-May-16	Female	700	140	Funnel trap
1114	3-May-16	Female	700	185	Funnel trap
1115	4-May-16	Female	545	80	Funnel trap
1115	12-May-16	Female	NA	NA	Funnel trap
1116	4-May-16	Male	450	51	Funnel trap
1117	4-May-16	Female	650	160	Funnel trap
1118	5-May-16	Male	385	30	Funnel trap
1119	10-May-16	Male	500	55	Funnel trap
1120	10-May-16	Male	455	50	Funnel trap
1120	12-May-16	Male	NA	NA	Funnel trap
1121	10-May-16	Male	510	68	Funnel trap
1121	18-May-16	Male	NA	NA	Funnel trap
1122	10-May-16	Female	465	46	Funnel trap
1122	11-May-16	Female	NA	NA	Funnel trap
1123	10-May-16	Male	450	40	Funnel trap
1124	10-May-16	Male	460	52	Funnel trap
1124	21-Apr-17	Male	525	55	Funnel trap
1124	22-Apr-17	Male	NA	NA	Funnel trap

ID	Date	Sex	SVL (mm)	Mass (g)	Method
1124	28-Apr-17	Male	NA	NA	Funnel trap
1125	10-May-16	Male	465	50	Funnel trap
1125	30-Apr-17	Male	510	45	Funnel trap
1126	11-May-16	Male	445	45	Funnel trap
1126	30-Apr-17	Male	495	42	Funnel trap
1127	11-May-16	Female	470	45	Funnel trap
1128	11-May-16	Male	450	40	Funnel trap
1129	11-May-16	Male	430	36	Funnel trap
1130	13-May-16	Male	450	45	Funnel trap
1131	15-May-16	Female	545	95	Funnel trap
1132	17-May-16	Male	540	70	Funnel trap
1133	17-May-16	Female	530	70	Funnel trap
1134	3-May-16	Male	450	39	Funnel trap
1134	24-May-16	Male	NA	NA	Funnel trap
1135	17-May-16	Male	440	55	Funnel trap
1135	28-Apr-17	Male	480	45	Funnel trap
1136	19-May-16	Male	450	45	Funnel trap
1137	21-May-16	Male	360	23	Funnel trap
1137	24-May-16	Male	NA	NA	Funnel trap
1138	22-May-16	Male	440	40	Funnel trap
1138	23-May-16	Male	NA	NA	Funnel trap
1139	24-May-16	Male	435	45	Funnel trap
1140	24-May-16	Male	480	48	Funnel trap
1142	20-Apr-17	Male	395	30	Funnel trap
1144	4-Apr-17	Male	530	48.5	Funnel trap
1145	5-Apr-17	Male	510	47	Funnel trap
1146	10-Apr-17	Female	580	140	Funnel trap
1147	17-May-17	Male	350	20	Funnel trap
1148	20-Apr-17	Female	435	37	Funnel trap
1149	10-Apr-17	Male	515	50	Funnel trap
1149	30-Apr-17	Male	NA	NA	Funnel trap
1149	1-May-17	Male	NA	NA	Funnel trap
1149	3-May-17	Male	NA	NA	Funnel trap
1150	14-Apr-17	Male	490	50	Funnel trap
1151	14-Apr-17	Male	415	38	Funnel trap
1151	1-May-17	Male	NA	NA	Funnel trap
1151	4-May-17	Male	NA	NA	Funnel trap
1151	7-May-17	Male	NA	NA	Funnel trap
1152	20-Apr-17	Male	480	41	Funnel trap
1152	21-Apr-17	Male	NA	NA	Funnel trap
1153	20-Apr-17	Male	510	40	Funnel trap
1153	4-May-17	Male	NA	NA	Funnel trap
1154	21-Apr-17	Male	460	40	Funnel trap
1154	28-Apr-17	Male	NA	NA	Funnel trap
1154	29-Apr-17	Male	NA	NA	Funnel trap
1155	22-Apr-17	Male	400	26	Funnel trap
1155	30-Apr-17	Male	NA	NA	Funnel trap
1156	22-Apr-17	Male	410	29	Funnel trap
1157	23-Apr-17	Female	485	65	Cover object
1157	27-Apr-17	Female	NA	NA	Funnel trap
1157	4-May-17	Female	NA	NA	Funnel trap
1157	9-May-17	Female	NA	NA	Funnel trap
1158	23-Apr-17	Male	520	45	Funnel trap
1159	25-Apr-17	Female	550	71	Cover object
1159	3-May-17	Female	NA	NA	Funnel trap
1159	4-May-17	Female	NA	NA	Funnel trap
1160	25-Apr-17	Male	490	48	Funnel trap
1160	28-Apr-17	Male	NA	NA	Funnel trap
1161	27-Apr-17	Male	465	36	Cover object

ID	Date	Sex	SVL (mm)	Mass (g)	Method
1161	28-Apr-17	Male	NA	NA	Funnel trap
1161	5-May-17	Male	NA	NA	Cover object
1161	12-May-17	Male	NA	NA	Funnel trap
1162	27-Apr-17	Female	465	40	Hand capture
1163	27-Apr-17	Male	485	40	Funnel trap
1164	27-Apr-17	Male	450	35	Funnel trap
1164	30-Apr-17	Male	NA	NA	Funnel trap
1164	1-May-17	Male	NA	NA	Funnel trap
1164	4-May-17	Male	NA	NA	Funnel trap
1165	27-Apr-17	Male	490	44	Funnel trap
1165	3-May-17	Male	NA	NA	Funnel trap
1165	7-May-17	Male	NA	NA	Funnel trap
1166	28-Apr-17	Male	355	20	Funnel trap
1167	28-Apr-17	Female	360	30	Funnel trap
1168	29-Apr-17	Male	385	18	Funnel trap
1169	29-Apr-17	Female	325	17	Funnel trap
1170	29-Apr-17	Male	500	50	Funnel trap
1170	30-Apr-17	Male	NA	NA	Funnel trap
1171	29-Apr-17	Female	550	118	Funnel trap
1171	1-May-17	Female	NA	NA	Funnel trap
1172	29-Apr-17	Male	425	28	Funnel trap
1173	29-Apr-17	Female	315	21	Funnel trap
1173	30-Apr-17	Female	NA	NA	Funnel trap
1174	29-Apr-17	Male	510	50	Funnel trap
1175	29-Apr-17	Female	590	108	Funnel trap
1175	6-May-17	Female	NA	NA	Funnel trap
1176	1-May-17	Male	515	45	Funnel trap
1177	1-May-17	Female	400	31	Funnel trap
1178	1-May-17	Female	550	100	Funnel trap
1179	1-May-17	Male	410	26	Funnel trap
1180	2-May-17	Male	555	72	Funnel trap
1181	3-May-17	Female	320	16	Cover object
1181	4-May-17	Female	NA	NA	Cover object
1181	9-May-17	Female	NA	NA	Cover object
1182	3-May-17	Female	355	20	Cover object
1182	4-May-17	Female	NA	NA	Cover object
1183	3-May-17	Male	530	50	Funnel trap
1183	4-May-17	Male	NA	NA	Funnel trap
1184	3-May-17	Male	420	28	Funnel trap
1185	4-May-17	Male	365	27	Cover object
1186	4-May-17	Female	370	25	Cover object
1187	4-May-17	Female	480	56	Funnel trap
1188	4-May-17	Male	520	41	Funnel trap
1188	18-May-17	Male	NA	NA	Funnel trap
1189	4-May-17	Female	585	120	Funnel trap
1190	5-May-17	Male	265	9	Hand capture
1191	7-May-17	Male	410	26	Funnel trap
1192	8-May-17	Female	390	30	Funnel trap
1193	8-May-17	Male	450	36	Funnel trap
1194	10-May-17	Male	440	33	Funnel trap
1194	13-May-17	Male	NA	NA	Funnel trap
1195	11-May-17	Female	560	100	Funnel trap
1196	11-May-17	Female	440	45	Funnel trap
1197	11-May-17	Male	400	29	Funnel trap
1197	15-May-17	Male	NA	NA	Funnel trap
1198	12-May-17	Female	360	18	Cover object
1198	16-May-17	Female	NA	NA	Cover object
1199	12-May-17	Female	405	37	Funnel trap
1200	12-May-17	Male	385	24	Funnel trap

ID	Date	Sex	SVL (mm)	Mass (g)	Method
1201	12-May-17	Female	410	38	Funnel trap
1202	15-May-17	Male	350	13	Funnel trap
1202	17-May-17	Male	NA	NA	Cover object
1203	15-May-17	Female	340	31	Cover object
1203	16-May-17	Female	NA	NA	Cover object
1204	15-May-17	Female	420	36	Cover object
1205	16-May-17	Female	375	28	Cover object
1206	17-May-17	Male	310	20	Funnel trap

Table 2. Summaries of trap array locations and habitat data at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014.

[Relative percent cover for each array was based on 12 random points (3 in each quadrant) located within 25 meters of the array. **Shannon index:** A measure of habitat diversity, calculated as $\sum_{i=1}^S p_i \ln p_i$, where S = number of habitats and p_i = proportion of habitat i at array. **Abbreviations and symbol:** Em. Veg., emergent vegetation; Herb. Terr. Veg., herbaceous terrestrial vegetation; Sub. Veg., submerged vegetation; Woody Veg., woody vegetation; m, meter; <, less than]

Array	Wetland association	Mean percent cover								Shannon index	Distance to wetland (m)
		Open water	Sub. Veg.	Em. Veg.	Herb. Terr. Veg.	Woody Veg.	Litter	Bare ground	Rock		
A	Aquatic Feature 4	0	0	0	72	19	9	0	0	0.333	71
B	Aquatic Feature 4	0	0	0	33	67	0	0	0	0.276	60
C	Aquatic Feature 3	0	0	0	64	36	0	0	0	0.285	61
D	Aquatic Feature 3	18	0	0	40	26	1	14	0	0.584	5
E	Aquatic Feature 3	0	0	0	98	2	0	1	0	0.058	89
F	Aquatic Feature 3	0	0	0	97	1	0	2	0	0.066	52
G	Aquatic Feature 1	0	0	0	40	55	3	3	0	0.382	30
H	Aquatic Feature 1	0	0	0	67	30	3	0	0	0.324	2
I	Aquatic Feature 1	0	0	0	55	38	6	1	0	0.392	31
J	Aquatic Feature 2	0	0	0	52	45	0	3	0	0.344	57
K	Aquatic Feature 2	3	0	46	50	1	0	0	0	0.369	2
L	Aquatic Feature 2	0	0	0	100	0	0	0	0	<0.001	39

Table 3. Summaries of trap array locations and habitat data at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2015.

[Relative percent cover for each array was based on 12 random points (3 in each quadrant) located within 25 meters of the array. **Shannon index:** A measure of habitat diversity, calculated as $\sum_{i=1}^S p_i \ln p_i$, where S = number of habitats and p_i = proportion of habitat i at array. **Abbreviations:** Em. Veg., emergent vegetation; Herb. Terr. Veg., herbaceous terrestrial vegetation; Sub. Veg., submerged vegetation; Woody Veg., woody vegetation; m, meter]

Array	Wetland association	Mean percent cover								Shannon index	Distance to wetland (m)
		Open water	Sub. Veg.	Em. Veg.	Herb. Terr. Veg.	Woody Veg.	Litter	Bare ground	Rock		
A	Aquatic Feature 4	0	0	0	78	17	5	1	0	0.685	71
B	Aquatic Feature 4	0	0	0	33	65	1	1	0	0.743	60
C	Aquatic Feature 3	0	0	0	77	23	0	0	0	0.543	61
D	Aquatic Feature 3	6	0	6	58	23	4	4	0	1.261	5
E	Aquatic Feature 3	0	0	0	92	0	4	4	0	0.358	89
F	Aquatic Feature 3	0	0	0	97	0	4	4	0	0.132	52
G	Aquatic Feature 1	0	0	0	50	50	0	0	0	0.693	30
H	Aquatic Feature 1	1	0	5	63	27	3	1	1	1.003	2
I	Aquatic Feature 1	0	0	0	66	33	0	1	0	0.703	31
J	Aquatic Feature 2	0	0	0	65	32	3	0	0	0.734	57
K	Aquatic Feature 2	3	0	43	50	1	2	0	0	0.962	2
L	Aquatic Feature 2	0	0	0	98	0	3	0	0	0.117	39

Table 4. Summaries of trap array locations and habitat data at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2016.

[Relative percent cover for each array was based on 12 random points (3 in each quadrant) located within 25 meters of the array. **Shannon index:** A measure of habitat diversity, calculated as $\sum_{i=1}^S p_i \ln p_i$, where S = number of habitats and p_i = proportion of habitat i at array. **Abbreviations:** Em. Veg., emergent vegetation; Herb. Terr. Veg., herbaceous terrestrial vegetation; Sub. Veg., submerged vegetation; Woody Veg., woody vegetation; m, meter]

Array	Wetland association	Mean percent cover								Shannon index	Distance to wetland (m)
		Open water	Sub. Veg.	Em. Veg.	Herb. Terr. Veg.	Woody Veg.	Litter	Bare ground	Rock		
A	Aquatic Feature 4	0	0	0	77	18	4	1	0	0.685	71
B	Aquatic Feature 4	0	0	0	32	68	0	0	0	0.627	60
C	Aquatic Feature 3	0	0	0	77	23	0	0	0	0.539	61
D	Aquatic Feature 3	8	0	8	57	23	1	2	1	1.233	5
E	Aquatic Feature 3	0	0	0	92	1	3	4	0	0.332	89
F	Aquatic Feature 3	0	0	0	100	0	0	0	0	0.000	52
G	Aquatic Feature 1	0	0	0	55	45	0	0	0	0.689	30
H	Aquatic Feature 1	1	0	8	59	27	3	1	1	1.086	2
I	Aquatic Feature 1	0	0	0	64	35	0	1	0	0.716	31
J	Aquatic Feature 2	0	0	0	63	34	3	0	0	0.750	57
K	Aquatic Feature 2	5	0	41	51	1	2	0	0	0.982	2
L	Aquatic Feature 2	0	0	0	97	0	3	0	0	0.122	39

Table 5. Summaries of trap array locations and habitat data at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2017.

[Relative percent cover for each array was based on 12 random points (3 in each quadrant) located within 25 meters of the array. **Shannon index:** A measure of habitat diversity, calculated as $\sum_{i=1}^S p_i \ln p_i$, where S = number of habitats and p_i = proportion of habitat i at array. **Abbreviations:** Em. Veg., emergent vegetation; Herb. Terr. Veg., herbaceous terrestrial vegetation; Sub. Veg., submerged vegetation; Woody Veg., woody vegetation; m, meter]

Array	Wetland association	Mean percent cover								Shannon index	Distance to wetland (m)
		Open water	Sub. Veg.	Em. Veg.	Herb. Terr. Veg.	Woody Veg.	Litter	Bare ground	Rock		
A	Aquatic Feature 4	0	0	0	75	22	2	1	0	0.665	71
B	Aquatic Feature 4	0	0	0	33	68	0	0	0	0.631	60
C	Aquatic Feature 3	0	0	3	74	23	0	0	0	0.671	61
D	Aquatic Feature 3	8	0	10	51	28	0	1	1	1.263	5
E	Aquatic Feature 3	0	0	0	90	4	3	4	0	0.446	89
F	Aquatic Feature 3	0	0	0	100	0	0	0	0	0.000	52
G	Aquatic Feature 1	0	0	0	55	45	0	0	0	0.687	30
H	Aquatic Feature 1	3	0	13	53	29	1	1	1	1.188	2
I	Aquatic Feature 1	0	0	0	67	32	0	1	0	0.672	31
J	Aquatic Feature 2	0	0	0	61	31	1	7	0	0.884	57
K	Aquatic Feature 2	7	0	39	49	1	1	3	0	1.085	2
L	Aquatic Feature 2	0	0	0	97	0	3	0	0	0.117	39

Sex Ratios and Size Distributions

Across all years of the study, the naïve sex ratio of San Francisco gartersnakes at Mindego Ranch was biased toward males, with a sex ratio of 1.6 (95-percent highest posterior density interval [hereinafter “HPDI”] = 1.3–2.0) males per female. The naïve sex ratio was unbiased in the first 2 years of the study (2014 = 0.7 [HPDI = 0.4–1.2] males per female; 2015 = 1.4 [HPDI = 0.8–2.6] males per female), but was biased toward males in the last 2 years of the study (2016 = 1.9 [HPDI = 1.3–2.8]; 2017 = 1.7 [HPDI = 1.2–2.4]; fig. 3).

Female San Francisco gartersnakes at Mindego Ranch were generally larger than males, with a mean SVL (514 [HPDI = 475–563] mm) 39 (HPDI = -6–88) mm longer than males (475 [HPDI = 459–491] mm), and a mean mass (78.3 [HPDI = 61.3–100.0] g) 27.3 (HPDI = 8.9–48.5) g greater than males (51.4 [HPDI = 47.4–55.5] g). Differences varied by year, however, with larger differences in size between males and females earlier in the study (table 6; figs. 4 and 5).

Table 6. Annual sex-specific mean San Francisco gartersnake (*Thamnophis sirtalis tetrataenia*) snout-vent length and mass at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[Differences are female minus male. Values in the table are posterior mean (numbers in parentheses are 95-percent highest posterior density interval).

Abbreviations: SVL; snout-vent length; g, gram; mm, millimeter]

Year	Male SVL (mm)	Female SVL (mm)	Difference in SVL	Male mass (g)	Female mass (g)	Difference in mass
2014	442 (388–502)	523 (448–607)	80 (-15–180)	36.6 (24.5–52.7)	67.2 (41.5–103.1)	30.6 (0.3–68.7)
2015	480 (445–516)	576 (514–642)	96 (-15–171)	52.3 (43.5–62.3)	106.4 (72.4–150.8)	54.2 (18.6–99.4)
2016	474 (459–490)	515 (473–561)	41 (-5–88)	51.2 (47.4–55.6)	78.4 (61.4–100.4)	27.1 (9.4–49.3)
2017	459 (437–482)	452 (416–490)	-7 (-49–37)	37.4 (32.9–42.2)	48.5 (37.0–62.6)	11.2 (-1.4–25.9)
Overall	475 (459–491)	514 (475–563)	39 (-6–88)	51.4 (47.4–55.5)	78.3 (61.3–100.0)	27.3 (8.9–48.5)

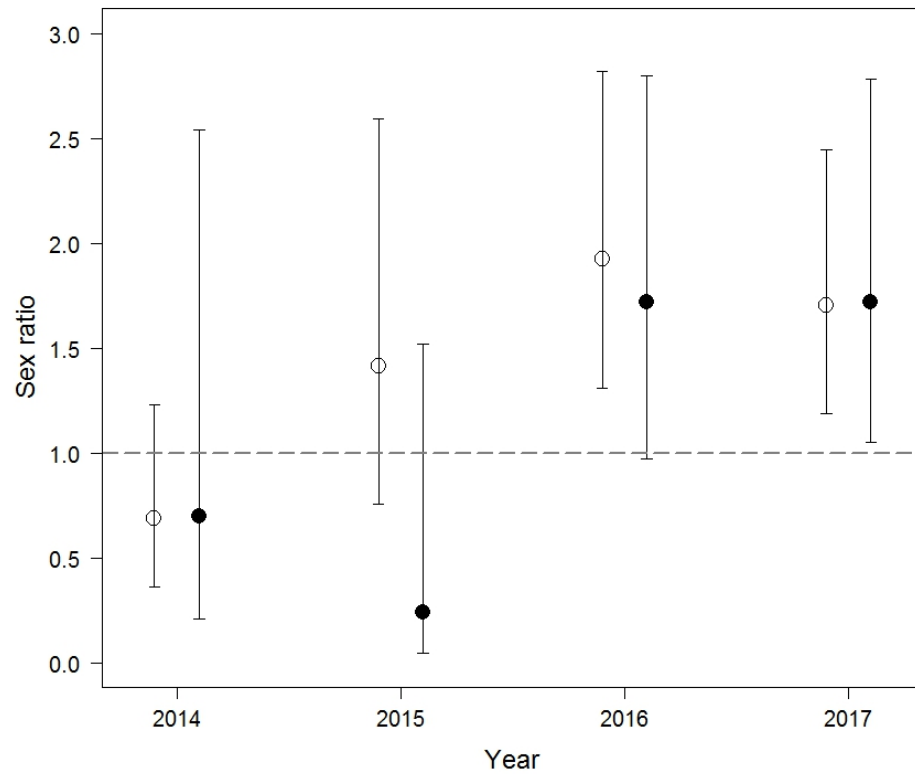
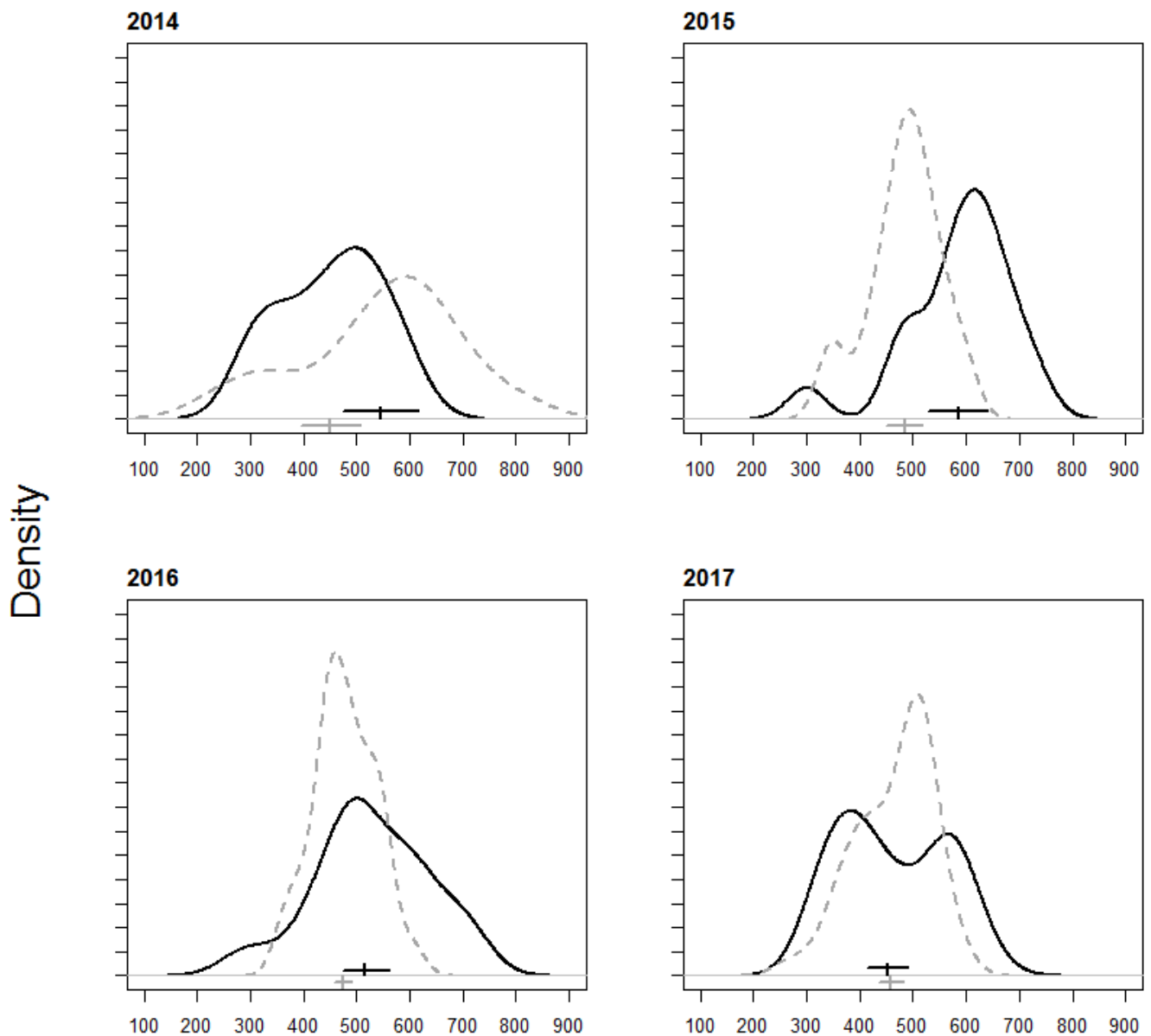


Figure 3. Graph showing annual sex ratios of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Closed dots represent posterior modes of sex ratios corrected for capture probabilities, and open dots represent posterior modes of naïve sex ratios; error bars represent 95-percent highest posterior density intervals.



Snout-vent length (mm)

Figure 4. Graphs showing annual kernel density plots of the distribution of San Francisco gartersnake (*Thamnophis sirtalis tetrataenia*) snout-vent length (in millimeters [mm]) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Solid black lines indicate females, dashed grey lines indicate males. Vertical bars along the x-axis indicate the posterior median of the mean; the horizontal bar associated with each median is the posterior 95-percent credible interval of the mean. Solid grey lines indicate the credible intervals of the mean for males.

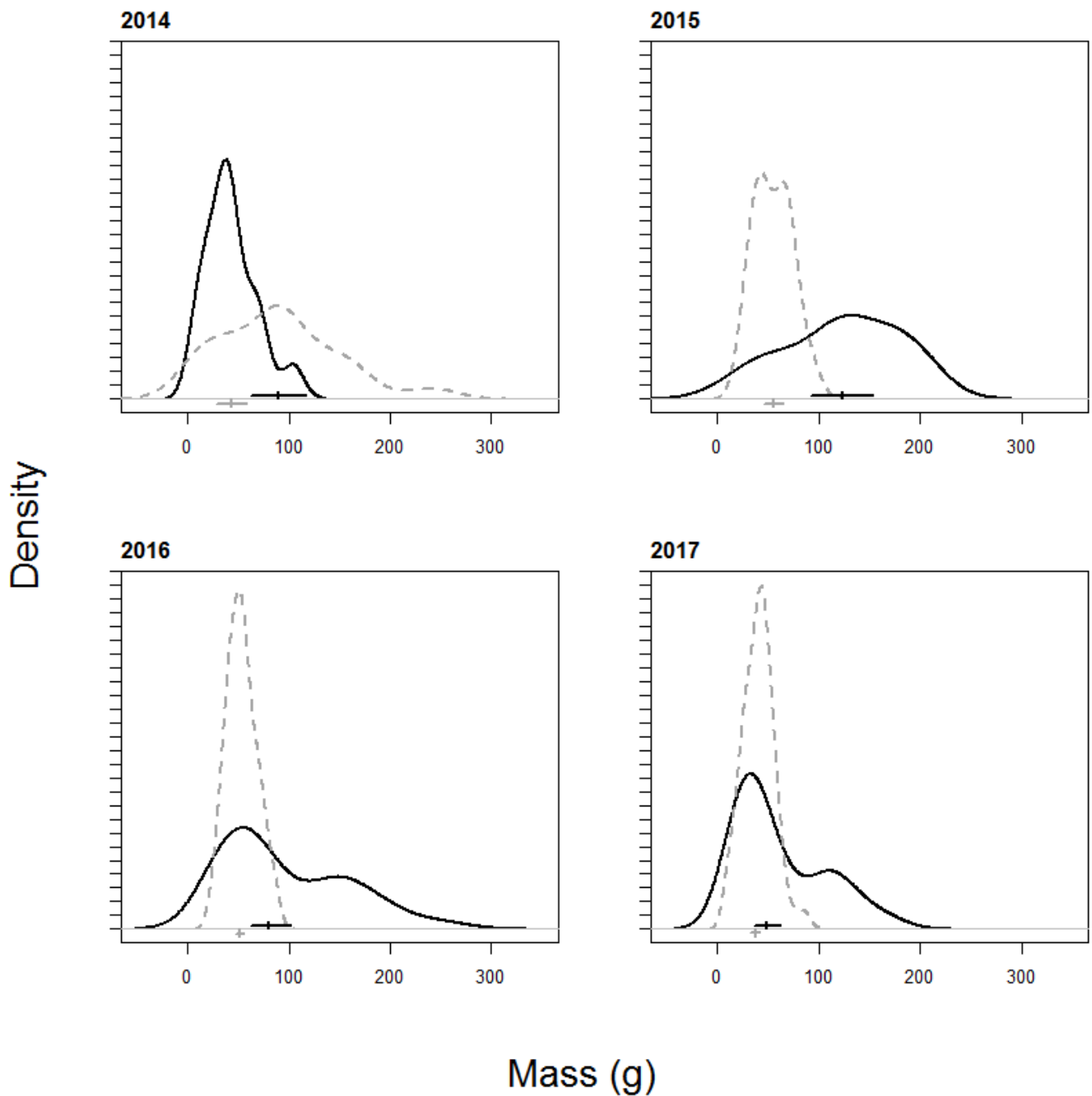


Figure 5. Graphs showing annual kernel density plots of the distribution of San Francisco gartersnake (*Thamnophis sirtalis tetrataenia*) mass (in grams [g]) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Solid black lines indicate females, dashed grey lines indicate males. Vertical bars along the x-axis indicate the posterior median of the mean; the horizontal bar associated with each median is the posterior 95-percent credible interval of the mean. Solid grey lines indicate the credible intervals of the mean for males.

Abundance and Demographic Rates

Closed Population Analysis

Abundance of San Francisco gartersnakes at Mindego Ranch based on closed population models fluctuated between 2014 and 2017. The model-averaged abundance of San Francisco gartersnakes at Mindego Ranch was 101 (HPDI = 53–225) individuals (41 [HPDI = 18–130] males and 53 [HPDI = 28–111] females) in 2014, 99 (HPDI = 54–364) individuals (36 [HPDI = 22–78] males and 48 [HPDI = 21–319] females) in 2015, 195 (HPDI = 146–292) individuals (126 [HPDI = 89–188] males and 69 [HPDI = 46–114] females) in 2016, and 137 (HPDI = 109–180) individuals (89 [HPDI = 68–117] males and 48 [HPDI = 36–69] females) in 2017 (fig. 6). Posterior probabilities for models that received the greatest support each year are shown in table 7. In 2014, the null model of constant capture probability (model where all coefficients = 0) had the highest posterior probability, but some support existed for an ephemeral behavioral response to avoid recapture (table 7, fig. 7). Capture probabilities increased with air temperature and males had higher capture probability than females (fig. 7) in 2015. In 2016 and 2017, San Francisco gartersnakes were more likely to be captured if they had been captured the previous day (fig. 7), and in 2017 capture probabilities also increased with air temperature (fig. 7). The logit-normal standard deviation of unexplained daily variation in capture probability was similar among years, although the precision with which random daily variation in capture probability was estimated varied among years (2014 = 0.00 [HPDI = 0.00–0.93]; 2015 = 0.95 [HPDI = 0.12–2.33]; 2016 = 0.90 [HPDI = 0.60–1.33]; 2017 = 0.98 [HPDI = 0.63–1.48]). The cumulative probability of capturing a given individual during the season was 0.35 (HPDI = 0.18–0.57) in 2014, 0.11 (HPDI = 0.03–0.48) in 2015, 0.40 (HPDI = 0.27–0.54) in 2016, and 0.50 (HPDI = 0.37–0.62) in 2017. The corrected (for capture probability) sex ratio of San Francisco gartersnakes at Mindego Ranch was 0.7 (HPDI = 0.2–2.5) males per female in 2014, 0.3 (HPDI = 0.1–1.6) in 2015, 1.7 (HPDI = 1.0–2.8) in 2016, and 1.7 (HPDI = 1.1–2.8) in 2017 (fig. 3).

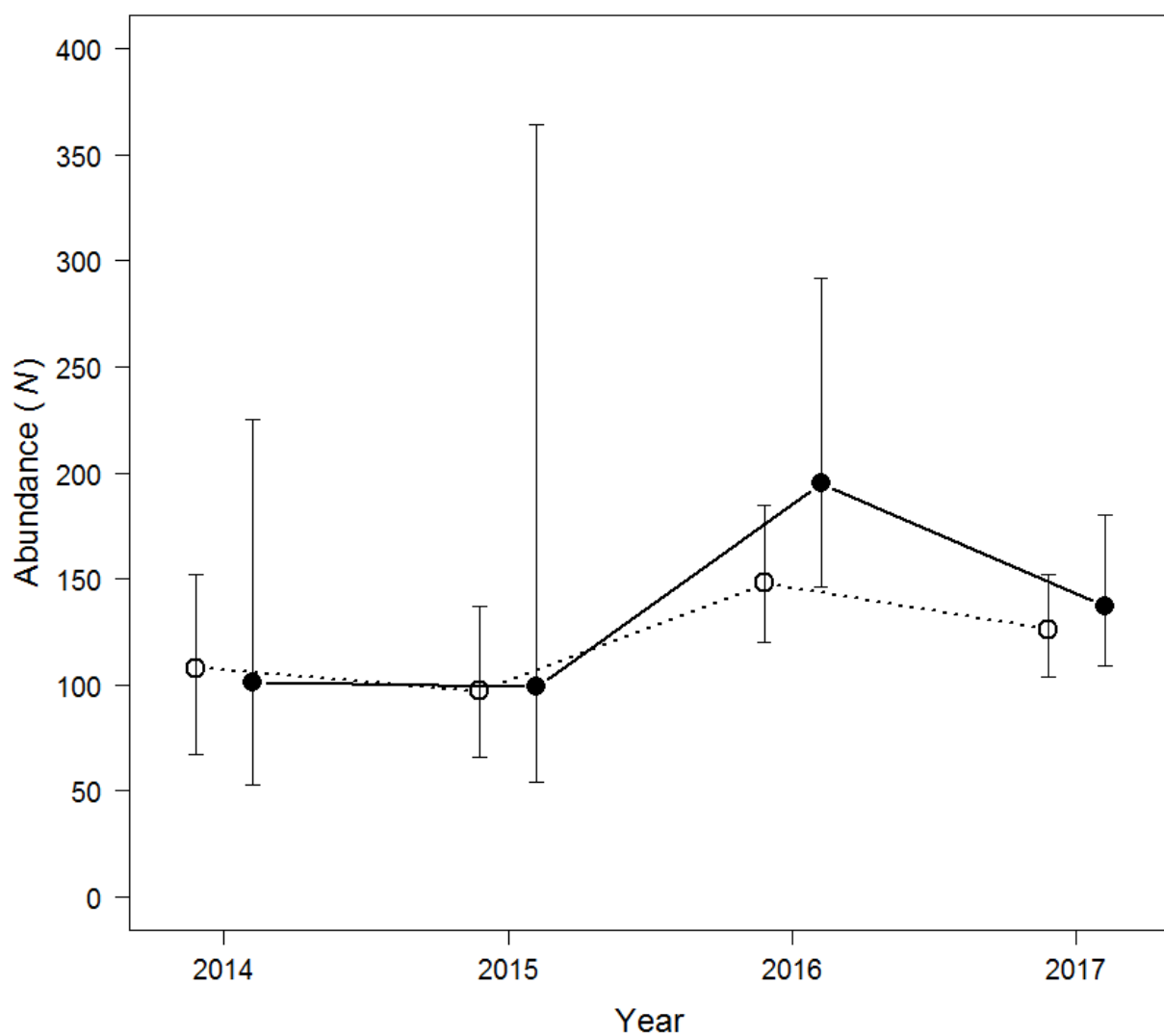


Figure 6. Graph showing annual abundance of San Francisco gartersnakes (N , number of gartersnakes; *Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Closed dots represent posterior modes from closed population analysis, and open dots represent posterior modes from open population analysis; error bars represent 95-percent highest posterior density intervals.

Table 7. Posterior probabilities of closed population models for abundance of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[A “1” indicates that the variable was included in the model; a “0” indicates that the variable was excluded from the model. Only models with a posterior probability greater than the prior probability for each model (0.03) are included. Models are shown in order of decreasing support. **Abbreviation:** SVL, snout-vent length]

Year	Variable					Posterior probability
	Air temperature	SVL	Sex	Behavioral response	Temporal heterogeneity	
2014	0	0	0	0	0	0.264
	0	0	0	1	0	0.221
	0	0	1	0	0	0.083
	0	0	1	1	0	0.067
	0	1	0	0	0	0.057
	0	1	0	1	0	0.049
	0	0	0	0	1	0.047
	0	0	0	1	1	0.035
	1	0	0	0	0	0.033
2015	1	0	1	0	1	0.279
	0	0	1	0	1	0.135
	1	0	1	1	1	0.110
	1	0	0	0	1	0.096
	1	1	1	0	1	0.078
	0	0	0	0	1	0.057
	0	0	1	1	1	0.056
	1	0	0	1	1	0.041
	0	1	1	0	1	0.036
2016	0	0	0	1	1	0.543
	1	0	0	1	1	0.252
	0	0	1	1	1	0.084
	0	1	0	1	1	0.047
	1	0	1	1	1	0.037
2017	1	0	0	1	1	0.844
	1	0	1	1	1	0.092
	1	1	0	1	1	0.051

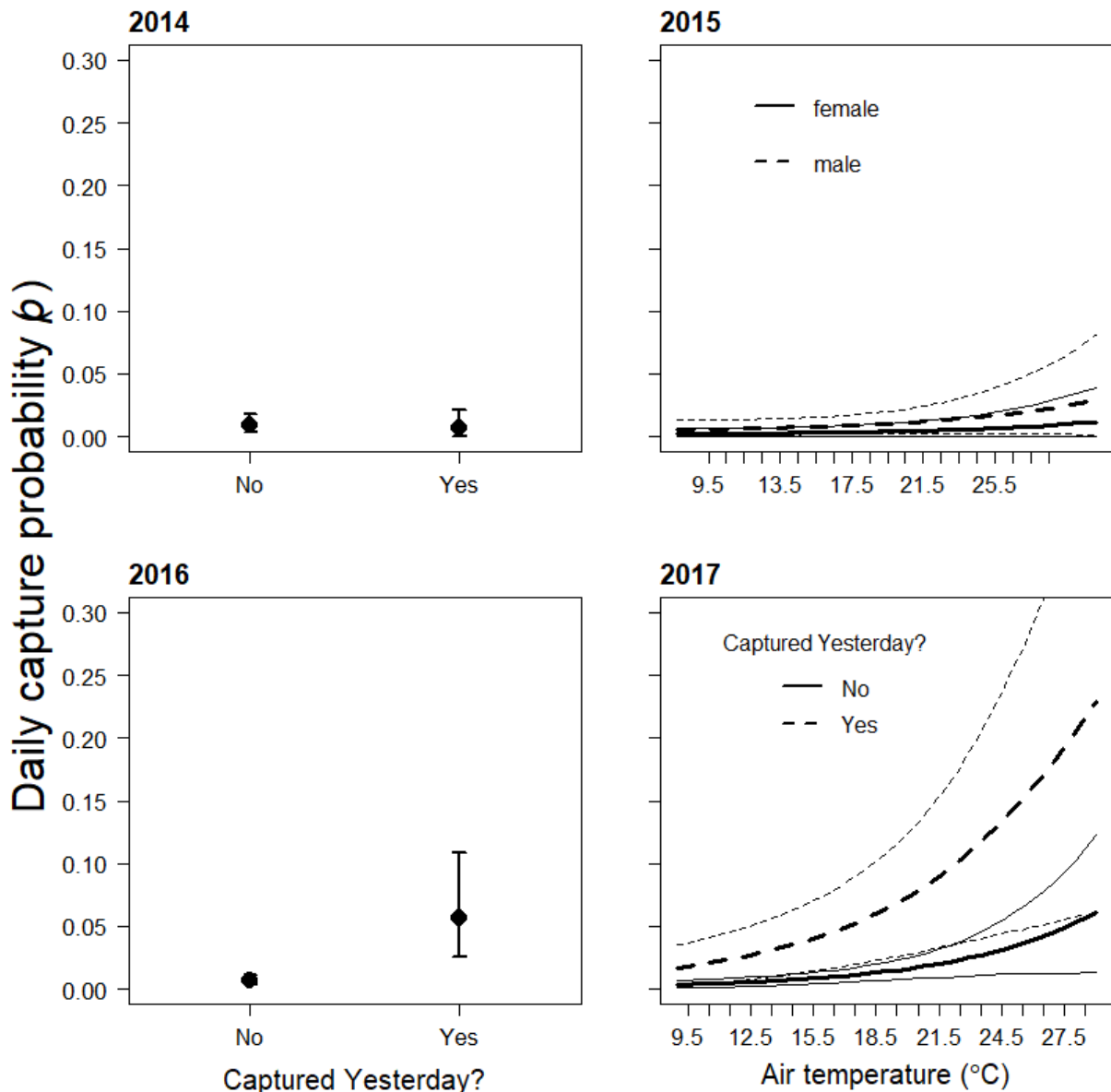


Figure 7. Graphs showing annual model-averaged effects of covariates on the capture probability of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Variables that contributed the most to the model each year are presented. Dots (2014 and 2016) and thick lines (2015 and 2017) represent posterior modes; error bars and thin lines represent 95-percent highest posterior density intervals. °C, degrees Celsius.

Open Population Analysis

The estimated annual abundance of San Francisco gartersnakes based on the Jolly-Seber open population model was 101 (HPDI = 67–152) snakes in 2014, 97 (HPDI = 66–137) snakes in 2015, 148 (HPDI = 120–185) snakes in 2016, and 126 (HPDI = 104–152) snakes in 2017 (fig. 6). The total number of individual snakes in the sampled area during April 2014–May 2017 was 311 (HPDI = 274–359). Annual apparent survival probability across all individuals was 0.64 (HPDI = 0.42–0.88) in 2014–15, 0.57 (HPDI = 0.36–0.79) in 2015–16, and 0.29 (HPDI = 0.18–0.43) in 2016–17 (fig. 8). Per-capita recruitment varied from year to year, and was 0.20 (HPDI = 0.00–0.69) in 2015, 0.86 (HPDI = 0.40–

1.61) in 2016, and 0.57 (HPDI = 0.35–0.78) in 2017 (fig. 9). Based on the Jolly-Seber model, daily capture probabilities varied little among years (2014 = 0.008 [HPDI = 0.006–0.014], 2015 = 0.009 [HPDI = 0.006–0.014], 2016 = 0.007 [HPDI = 0.005–0.009], and 2017 = 0.008 [HPDI = 0.006–0.010]; fig. 10), and cumulative capture probabilities were 0.32 (HPDI = 0.24–0.48), 0.34 (HPDI = 0.26–0.50), 0.57 (HPDI = 0.46–0.66), and 0.64 (HPDI = 0.55–0.73) in 2014, 2015, 2016, and 2017, respectively (fig. 11). The intrinsic population growth rate was stable in 2014–15 (–0.08 [HPDI = –0.51–0.37]), positive in 2015–16 (HPDI = 0.37 [0.01–0.85]), and slightly negative in 2016–17 (HPDI = –0.16 [–0.45–0.10]; fig. 12). The mean population growth rate from 2014 through 2017 was 0.04 (HPDI = –0.08–0.20). The probability that the population was stable (less than 10-percent annual change in abundance) was 0.72, which was higher than the probability that abundance increased by more than 10-percent annually (0.27) or the probability that abundance decreased by more than 10-percent annually (0.01). A 10-percent increase in abundance was 40 times more likely than a 10-percent decrease in abundance, and the population was 12 times more likely to be increasing (by any amount) or stable than decreasing between 2014 and 2017.

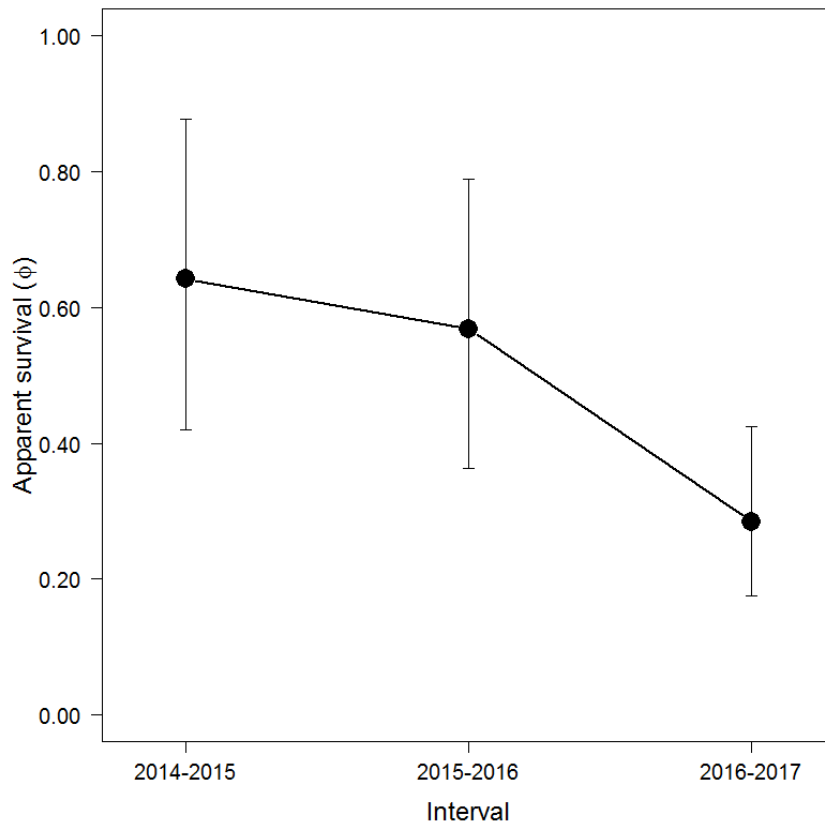


Figure 8. Graph showing annual apparent survival probabilities of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

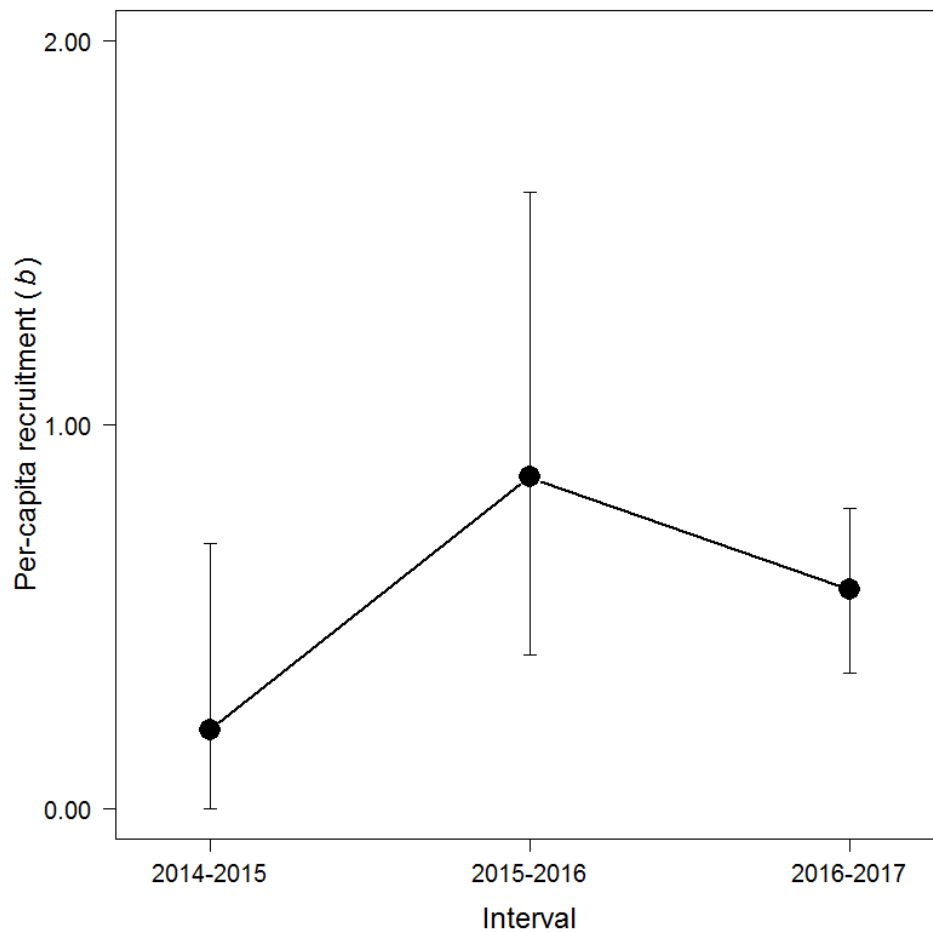


Figure 9. Graph showing annual per-capita recruitment of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014– 17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

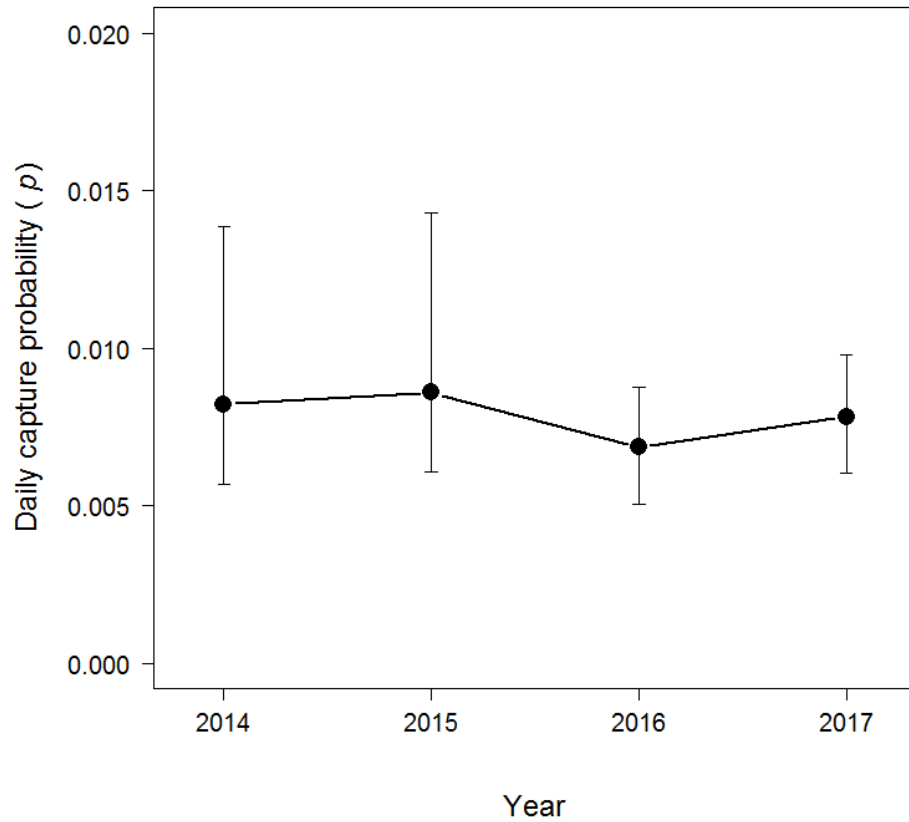


Figure 10. Graph showing annual daily capture probabilities of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

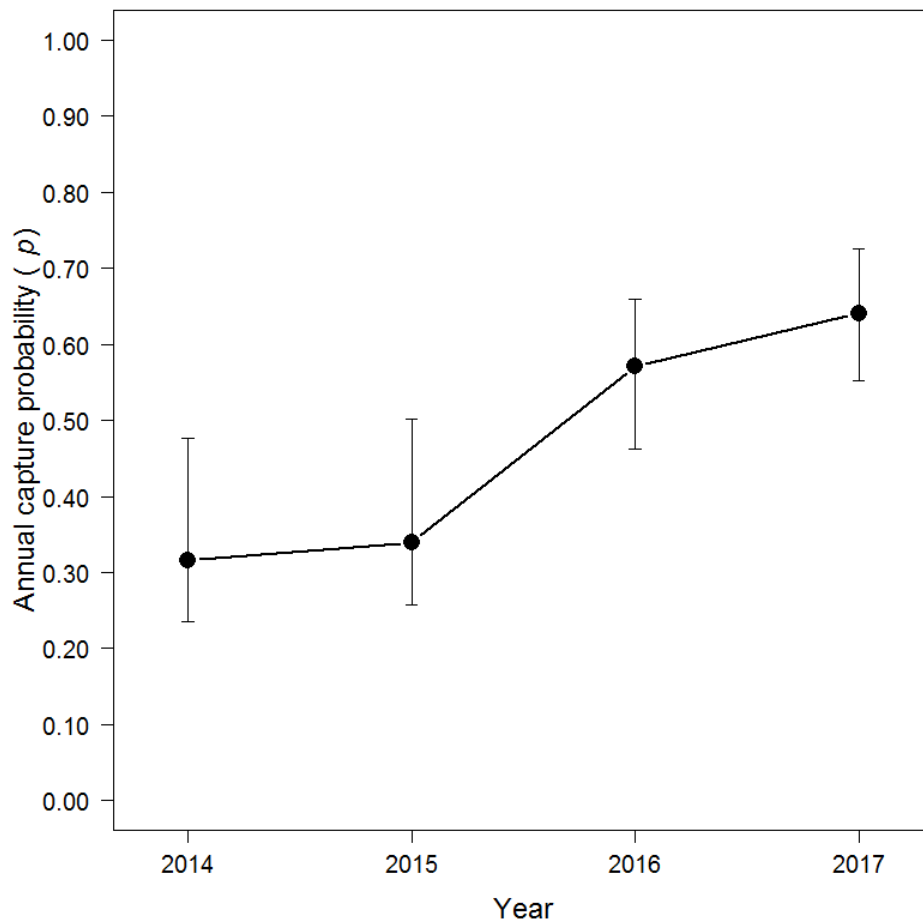


Figure 11. Graph showing annual capture probabilities of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes of cumulative capture probabilities; error bars represent 95-percent highest posterior density intervals.

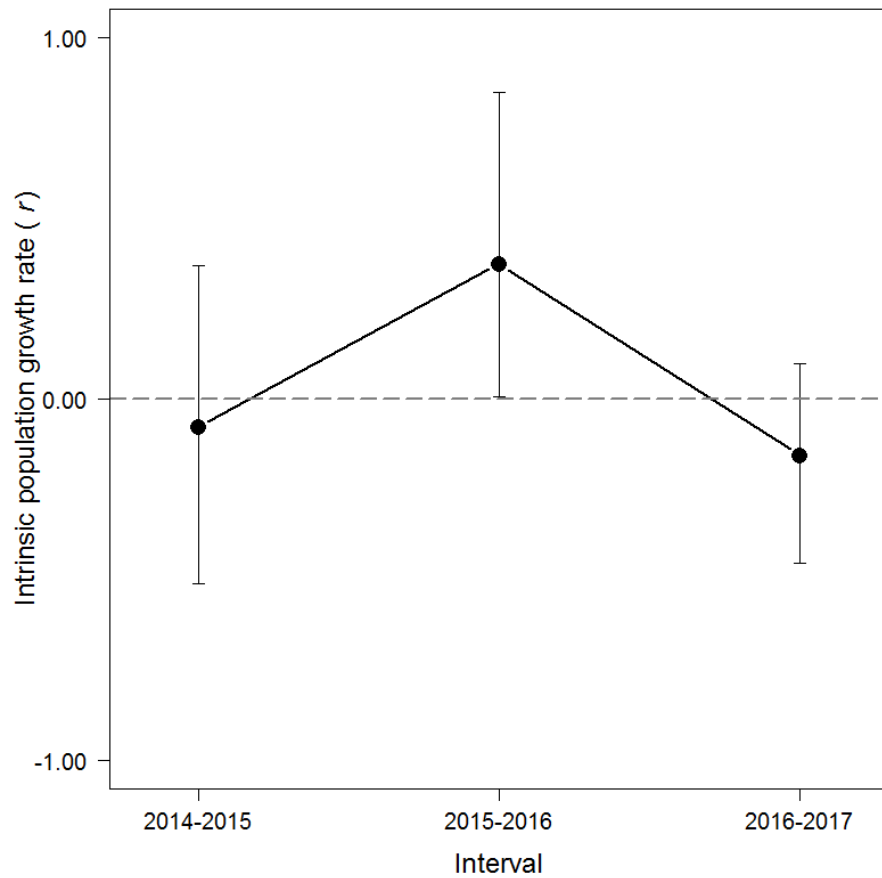


Figure 12. Graph showing annual intrinsic population growth rate of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindogo Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals. The horizontal dashed line at 0.00 represents no population change.

Spatial Distribution

Static Occupancy Models

The best-fit detection component for the single-season occupancy models for San Francisco gartersnakes included site heterogeneity and a negative effect of rain on p for all years (table 8; fig. 13). The standard deviation describing the logit-normal variation among sites in p was 0.99 (HPDI = <0.01–3.17) in 2014, 1.95 (HPDI = 0.67–5.29) in 2015, 2.07 (HPDI = 1.11–4.19) in 2016, and 2.23 (HPDI = 1.22–4.57) in 2017. The best-fit model of occurrence for 2014–16 was the null model of equal probability of occurrence among arrays (models where both coefficients = 0; table 9). Evidence existed for a positive effect of habitat diversity on occurrence probability in 2017 (table 9). The probability of occurrence for San Francisco gartersnakes at trap arrays within 100 m of wetlands at Mindego Ranch and the number of the trap arrays estimated to be occupied during the sampling period are summarized in table 10.

Table 8. Posterior probabilities for models of daily detection probabilities for occurrence of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) in trap arrays at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[A “1” indicates that the variable was included in the model; a “0” indicates that the variable was excluded from the model. Only models with a posterior probability greater than the prior probability for each model (0.063) and the null model are included. Models are shown in order of decreasing support. **Symbol:** <, less than]

Year	Variable				Posterior probability
	Air temperature	Rain	Site heterogeneity	Temporal heterogeneity	
2014	0	1	1	0	0.285
	0	1	1	1	0.203
	0	0	1	0	0.164
	0	0	1	1	0.129
	1	1	1	0	0.074
	0	0	0	0	<0.01
2015	0	1	1	0	0.282
	0	1	1	1	0.156
	1	1	1	0	0.134
	0	0	1	0	0.128
	1	0	1	0	0.086
	1	1	1	1	0.077
	0	0	0	0	<0.01
2016	0	1	1	0	0.496
	0	1	1	1	0.218
	1	1	1	0	0.196
	1	1	1	1	0.082
	0	0	0	0	<0.01
2017	0	1	1	1	0.751
	1	1	1	1	0.134
	0	1	1	0	0.098
	0	0	0	0	<0.01

Table 9. Posterior probabilities for models of occurrence probability of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) in trap arrays at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[A “1” indicates that the variable was included in the model; a “0” indicates that the variable was excluded from the model. Only models with a posterior probability greater than the prior probability for each model (0.25) and the null model are included. Models are shown in order of decreasing support]

Year	Variable		Posterior probability
	Habitat heterogeneity	Site heterogeneity	
2014	0	0	0.407
2015	0	0	0.341
	1	1	0.271
2016	0	0	0.437
2017	1	0	0.350
	0	0	0.243

Table 10. Posterior summaries of occurrence probabilities and the estimated number of trap arrays occupied for the single-season occupancy model fitted to the San Francisco gartersnake population at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[Values in the table are for posterior mode (numbers in parentheses are 95-percent highest posterior density interval).
Symbol: Ψ , occurrence probability]

Year	Ψ	Number of occupied arrays
2014	0.90 (0.49–1.00)	10 (7–12)
2015	0.40 (0.13–0.87)	4 (4–9)
2016	0.63 (0.35–0.94)	7 (7–11)
2017	0.70 (0.40–1.00)	7 (7–11)

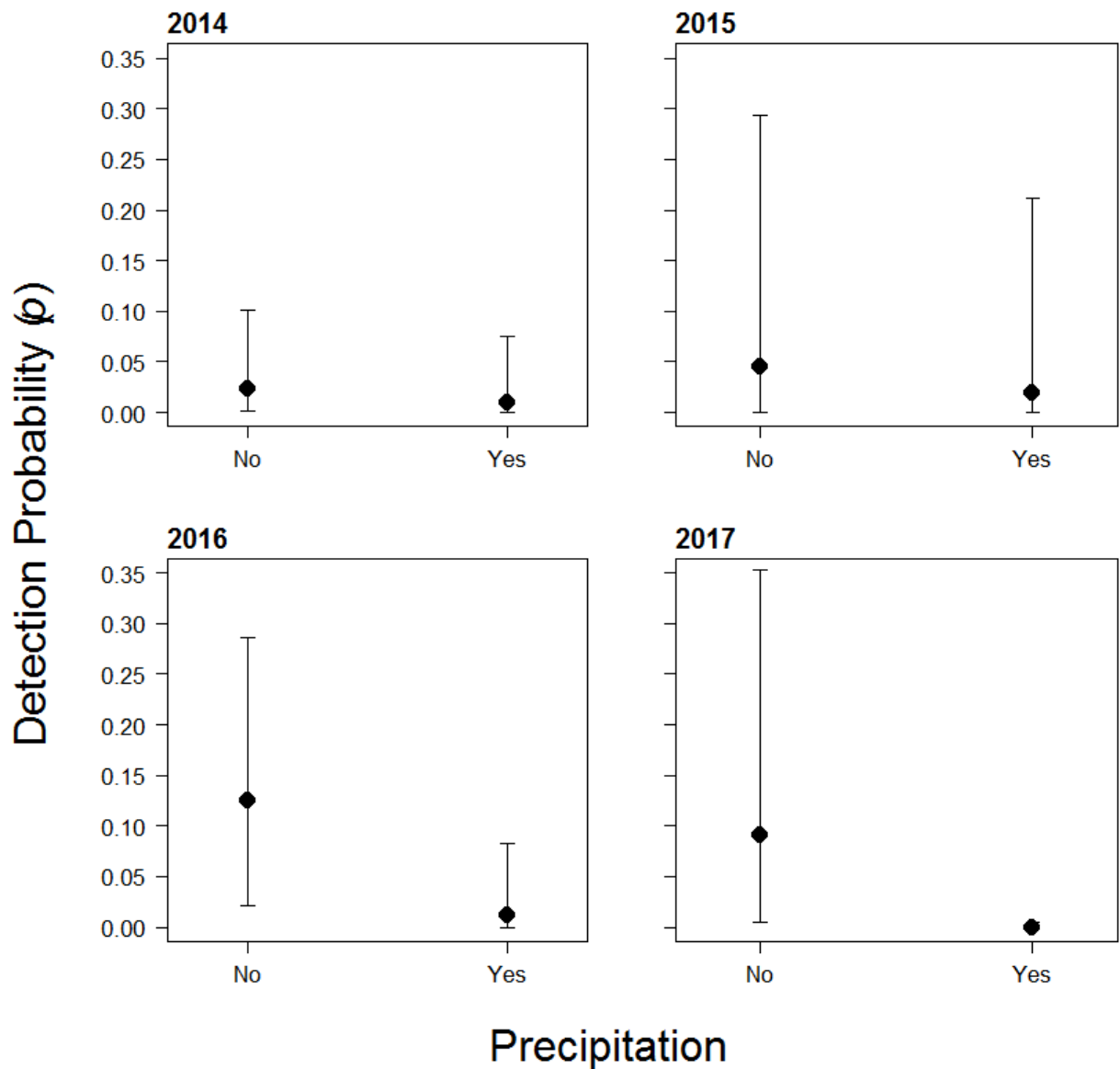


Figure 13. Graphs showing effect of precipitation on detection probability of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindogo Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

Binomial Mixture Models

Habitat composition varied among trap arrays, as did the number of San Francisco gartersnake captures (table 11). The best-supported detection probability models included a negative effect of rain on p in 2014 and a positive effect of air temperature and temporal heterogeneity on p in all other years (table 12; figs. 14 and 15). The proportional abundance model that received the most support in 2014 included random, unexplained variation in abundance among arrays and a positive effect of habitat diversity on abundance (table 13). For every increase of 0.17 in the Shannon-Weaver diversity index in 2014, predicted mean proportional abundance of San Francisco gartersnakes increased by a factor of 1.35 (HPDI = 0.73–6.76; fig. 16). During 2015–17, the proportional abundance model that received the highest support included random variation in abundance among arrays, but some support existed for a positive effect of habitat diversity on proportional abundance in each year (table 13). In each year of the study, San Francisco gartersnake activity was greatest at Array D, and in all years except 2014, it was second-greatest at Array C (table 11; fig. 17).

Table 11. Raw counts of captures and estimates of proportional abundance of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at each trap array based on the best-fit binomial mixture model at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[Proportional abundance estimates are presented as posterior mode (numbers in parentheses are 95-percent highest posterior density interval). **Symbol:** <, less than]

Array	Total captures				Proportional abundance			
	2014	2015	2016	2017	2014	2015	2016	2017
A	0	0	0	0	<0.01 (<0.01–0.06)	<0.01 (<0.01–0.04)	<0.01 (<0.01–0.02)	<0.01 (<0.01–0.02)
B	1	1	2	0	0.02 (<0.01–0.07)	0.02 (0.01–0.09)	0.01 (<0.01–0.02)	<0.01 (<0.01–0.02)
C	2	5	22	36	0.03 (<0.01–0.1)	0.13 (0.04–0.25)	0.20 (0.13–0.28)	0.32 (0.24–0.41)
D	24	23	64	40	0.61 (0.45–0.77)	0.71 (0.56–0.85)	0.60 (0.50–0.69)	0.36 (0.27–0.45)
E	1	2	8	24	0.01 (<0.01–0.06)	0.04 (<0.01–0.13)	0.06 (0.02–0.11)	0.21 (<0.01–0.02)
F	1	0	5	0	0.01 (<0.01–0.06)	<0.01 (<0.01–0.03)	0.05 (0.01–0.08)	<0.01 (<0.01–0.016)
G	3	0	0	3	0.07 (0.02–0.14)	<0.01 (<0.01–0.04)	<0.01 (<0.01–0.02)	0.03 (<0.01–0.06)
H	1	0	5	1	0.03 (<0.01–0.09)	<0.01 (<0.01–0.04)	0.04 (0.01–0.07)	0.01 (<0.01–0.04)
I	0	0	0	1	0.01 (<0.01–0.09)	<0.01 (<0.01–0.04)	<0.01 (<0.01–0.02)	0.01 (<0.01–0.03)
J	0	0	0	0	0.01 (<0.01–0.064)	<0.01 (<0.01–0.04)	<0.01 (<0.01–0.02)	<0.01 (<0.01–0.02)
K	2	0	2	5	0.06 (0.01–0.13)	<0.01 (<0.01–0.04)	0.02 (<0.01–0.05)	0.04 (0.02–0.09)
L	0	0	0	0	<0.01 (<0.01–0.03)	<0.01 (<0.01–0.03)	<0.01 (<0.01–0.02)	<0.01 (<0.01–0.02)
Total	34	31	108	110	1.0	1.0	1.0	1.0

Table 12. Posterior probabilities for 5-day period detection probabilities for binomial mixture models of array-specific proportional abundance of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[A “1” indicates that the variable was included in the model; a “0” indicates that the variable was excluded from the model. Only models with a posterior probability greater than the prior probability for each model (0.125) and the null model are included. Models are shown in order of decreasing support. Note that sampling periods were 6 days instead of 5 days in 2017. **Symbol:** <, less than]

Year	Variable			Posterior probability
	Air temperature	Rain	Temporal heterogeneity	
2014	0	1	0	0.524
	1	1	0	0.161
	0	1	1	0.160
	0	0	0	0.028
2015	1	0	1	0.381
	0	0	1	0.221
	1	1	1	0.180
	0	0	0	0.006
2016	1	0	1	0.358
	0	0	1	0.348
	1	1	1	0.151
	0	1	1	0.144
	0	0	0	<0.001
2017	1	0	1	0.367
	0	1	1	0.263
	1	1	1	0.232
	0	0	1	0.138
	0	0	0	<0.001

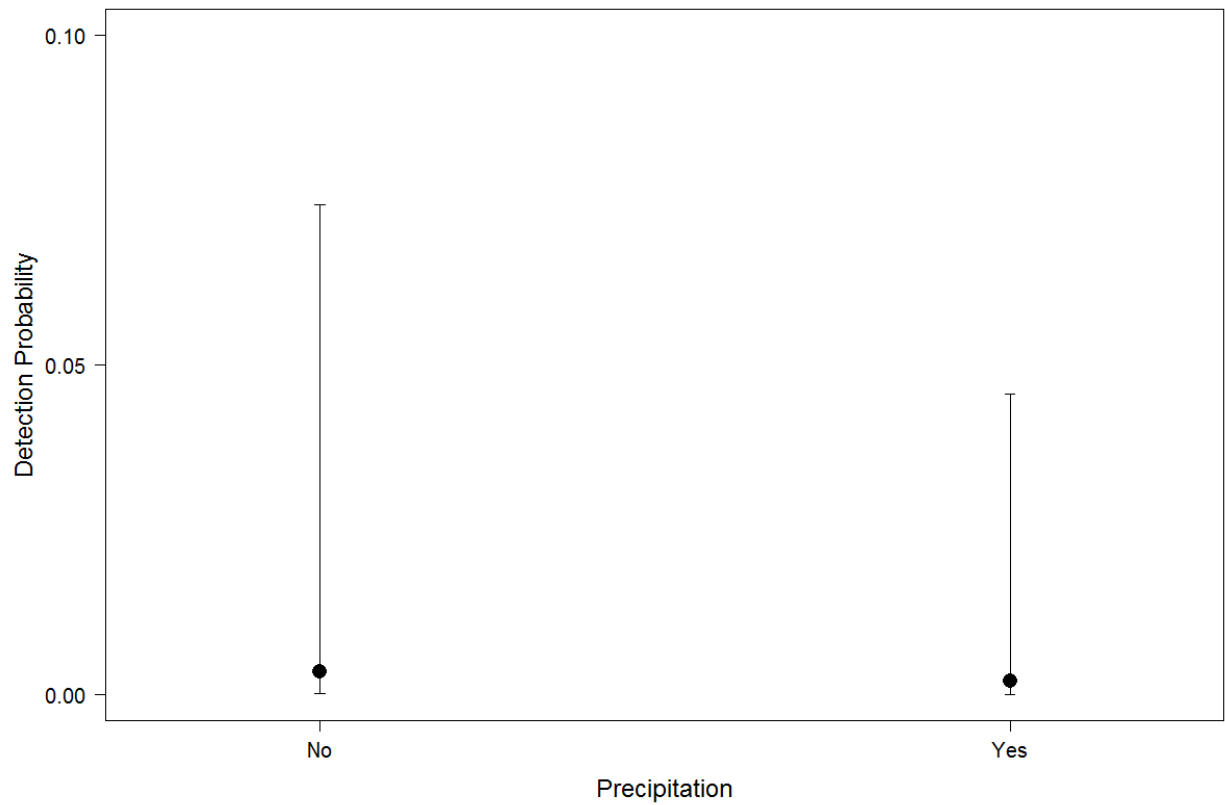


Figure 14. Graph showing effect of precipitation on 5-day detection probability of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindogo Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014. Dots indicate posterior medians, and light lines indicate 95-percent credible intervals.

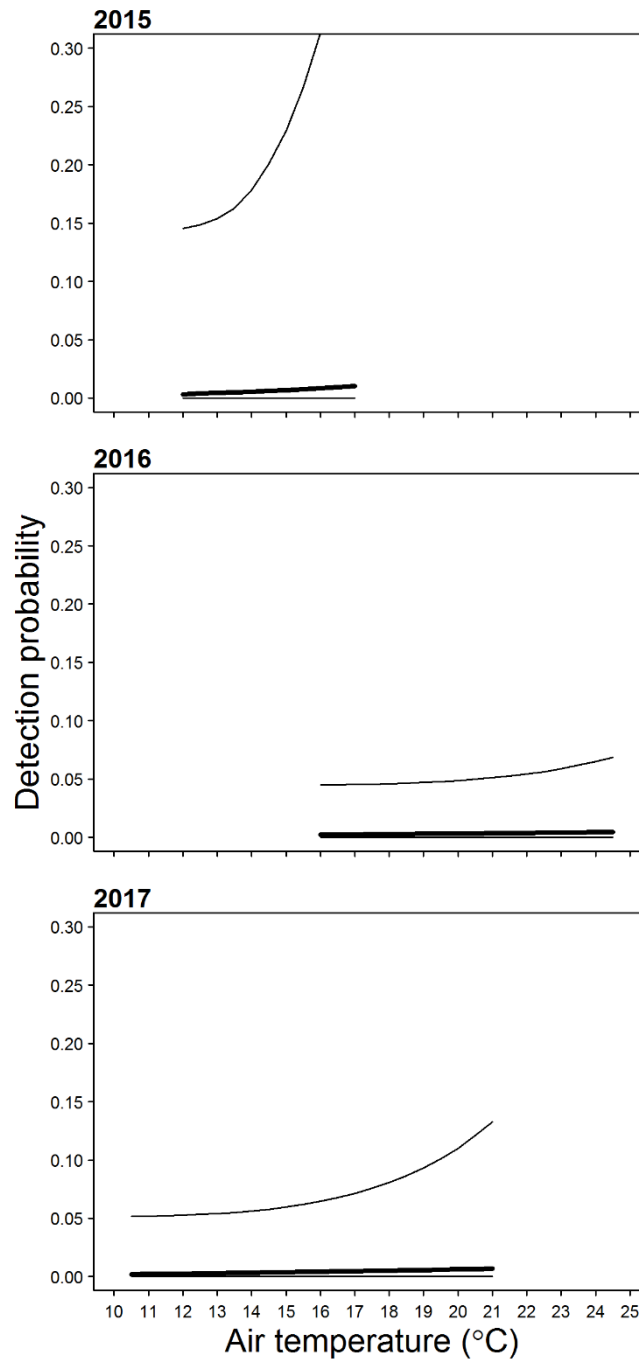


Figure 15. Graphs showing effect of mean air temperature (in degrees Celsius [°C]) on 5-day (2015 and 2016) or 6-day (2017) detection probability of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2015–17. Bold lines indicate posterior medians; light lines indicate 95-percent credible intervals.

Table 13. Posterior probabilities for binomial mixture models of array-specific proportional abundance of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[A “1” indicates that the variable was included in the model; a “0” indicates that the variable was excluded from the model. Only models with a posterior probability greater than the prior probability for each model (0.125) and the null model are included. Models are shown in order of decreasing support. **Symbol:** <, less than]

Year	Variable			Posterior probability
	Habitat diversity	Distance to water	Site heterogeneity	
2014	1	0	1	0.356
	1	1	1	0.171
	0	0	1	0.136
	0	0	0	<0.001
2015	0	0	1	0.361
	1	0	1	0.261
	1	1	1	0.188
	0	1	1	0.184
	0	0	0	<0.001
2016	0	0	1	0.420
	1	0	1	0.228
	0	1	1	0.208
	1	1	1	0.144
	0	0	0	<0.001
2017	0	0	1	0.368
	1	0	1	0.278
	0	1	1	0.180
	1	1	1	0.175
	0	0	0	<0.001

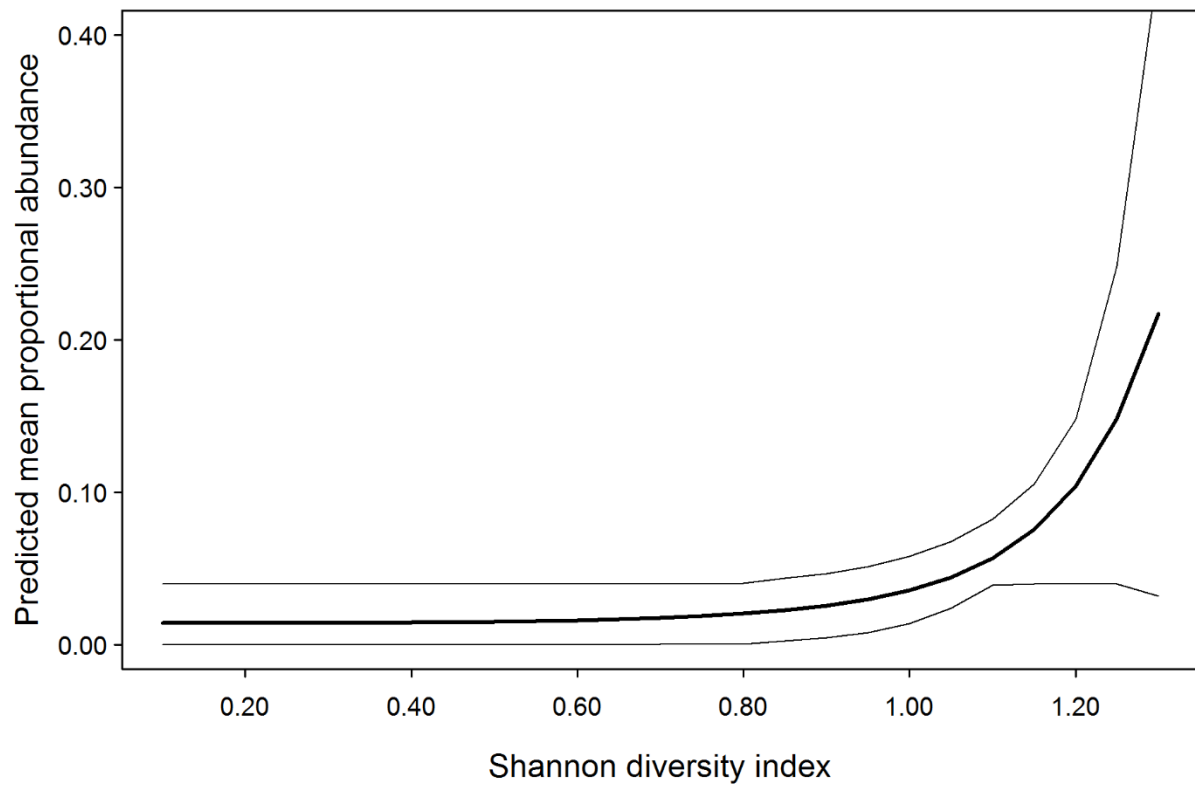


Figure 16. Graph showing predicted mean proportional abundance of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) as a function of the diversity of habitats within 25 meters of the array at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014. Bold line indicates posterior median; light lines indicate the 95-percent credible interval.

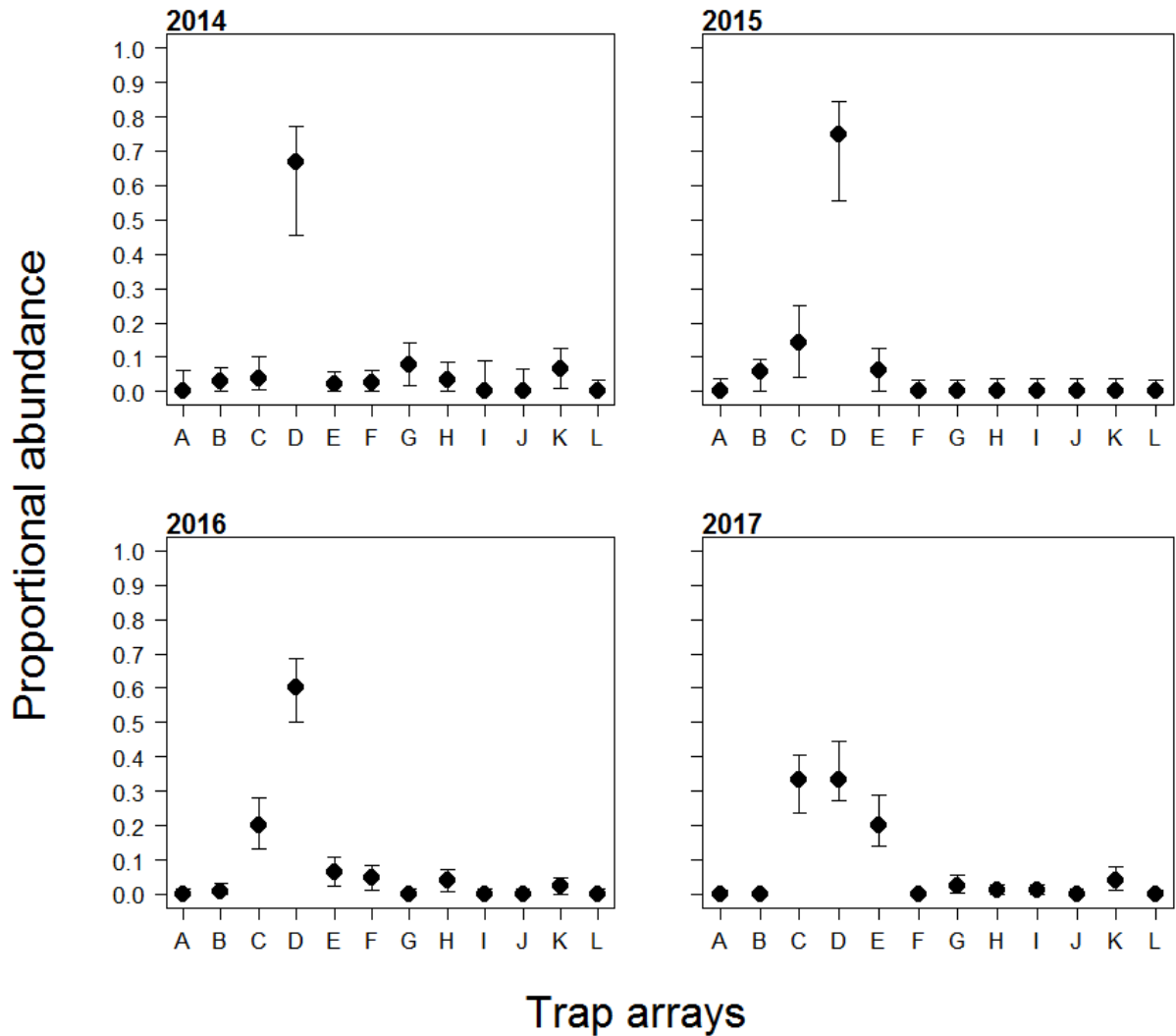


Figure 17. Graphs showing annual proportional abundance of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) for each array at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

Dynamic Occupancy Analysis

The dynamic occupancy model that received the greatest support (highest posterior probability) included heterogeneity in initial occupancy probability (ψ), an effect of distance to wetland on the probability of colonization (γ), and effects of habitat heterogeneity and distance to wetland interacting to affect persistence ($\phi = 1 - \text{the probability of extirpation } [\varepsilon]$; table 14). The occurrence probability of San Francisco gartersnakes was the lowest in 2017 (HPDI = 0.47 [0.14–0.82]) and highest in 2014 (HPDI = 0.70 [0.32–0.97]; table 15, fig. 18). The probability that arrays occupied in one year become unoccupied the next year was stable across years (fig. 19), but varied with array characteristics. At arrays near water, habitat diversity increased the probability that arrays occupied in one year would remain occupied the next year, but this relation was reversed and much more uncertain farther from water (fig. 20). Similarly, in arrays with high habitat diversity, arrays near water were more likely to remain occupied; this relation was reversed for arrays with low habitat diversity (fig. 20). The probability that arrays unoccupied in one year were colonized by the next year was similar across years (fig. 21). Unoccupied arrays near water were more likely to be colonized than arrays far from water (fig. 22). Similarly, with every 28 m distance from a wetland, unoccupied arrays were 0.12 (HPDI = 0.02–1.0) times as likely to be colonized (fig. 22). The probability that an occupied array in one year is a newly occupied one (turnover probability) was the highest in 2017 (fig. 23), as was the occupancy growth rate (fig. 24). Mean daily detection probability was stable throughout the study (fig. 25). The mean annual probability of occurrence during 2014–17 was more likely to be decreasing by more than 10-percent annually (0.51) than it was to be stable (0.41) or increasing by more than 10-percent annually (0.09). The number of occupied arrays was highest in 2014 and lowest in 2015 (fig. 26), and the finite-sample occupancy growth rate was negative during 2014–15, positive in 2015–16, and stable in 2016–17 (fig. 27). The probability that the number of occupied sites was stable (0.97) was greater than the probability that it decreased (0.03) or increased (<0.01) annually by 10-percent or more.

Table 14. Posterior probabilities for models of initial occurrence, persistence, and colonization of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) in trap arrays at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[A “1” indicates that the variable was included in the model; a “0” indicates that the variable was excluded from the model. Only models with a posterior probability greater than their prior probability and the null model are included. Models are shown in order of decreasing support. Abbreviation: NA, not applicable]

Parameter	Variable					Posterior probability
	Habitat diversity	Distance to wetland	Habitat heterogeneity by distance to wetland	Array heterogeneity	Annual heterogeneity	
Initial occurrence (ψ)	0	0	0	1	NA	0.198
	0	0	0	0	NA	0.172
	1	0	0	1	NA	0.140
Colonization (Υ)	0	1	0	0	0	0.135
	0	1	0	1	0	0.110
	0	1	0	0	1	0.093
	0	1	0	1	1	0.082
	1	1	1	0	0	0.081
	1	1	1	1	0	0.066
	1	1	1	0	1	0.064
	1	1	1	1	1	0.054
	0	0	0	0	0	0.020
Persistence (ϕ)	1	1	1	0	0	0.213
	1	1	1	1	0	0.198
	1	1	1	0	1	0.158
	1	1	1	1	1	0.148
	0	0	0	0	0	0.010

Table 15. Posterior summaries of annual occupancy probability, number of occupied arrays, colonization probability, and persistence probability from the dynamic occupancy model for San Francisco gartersnakes at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[Parameter estimates are presented as posterior mode (95-percent highest posterior density interval). **Symbols:** Ψ , annual occupancy probability; γ , colonization probability; Φ , persistence probability; <, less than; >, greater than; NA, not applicable]

Year	Ψ	Number of occupied arrays	γ	Φ
2014	0.70 (0.32–0.97)	8 (8–9)	NA	0.74 (0.24–>0.99)
2015	0.56 (0.21–0.87)	4 (4–4)	0.24 (0.02–0.84)	0.73 (0.16–0.98)
2016	0.50 (0.17–0.84)	7 (7–7)	0.24 (<0.01–0.73)	0.75 (0.30–>0.99)
2017	0.47 (0.14–0.82)	7 (7–7)	0.23 (<0.01–0.64)	NA

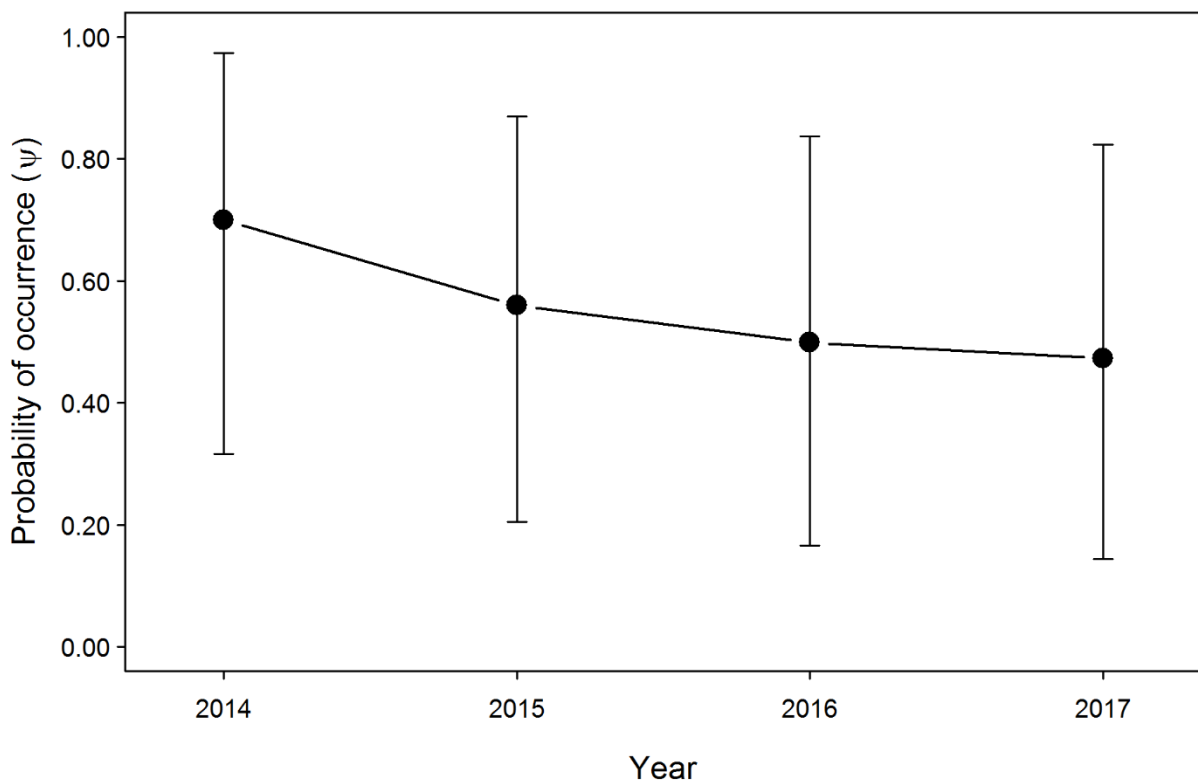


Figure 18. Graph showing annual probability of occurrence of San Francisco gartersnakes at trap arrays based on the dynamic occupancy model at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

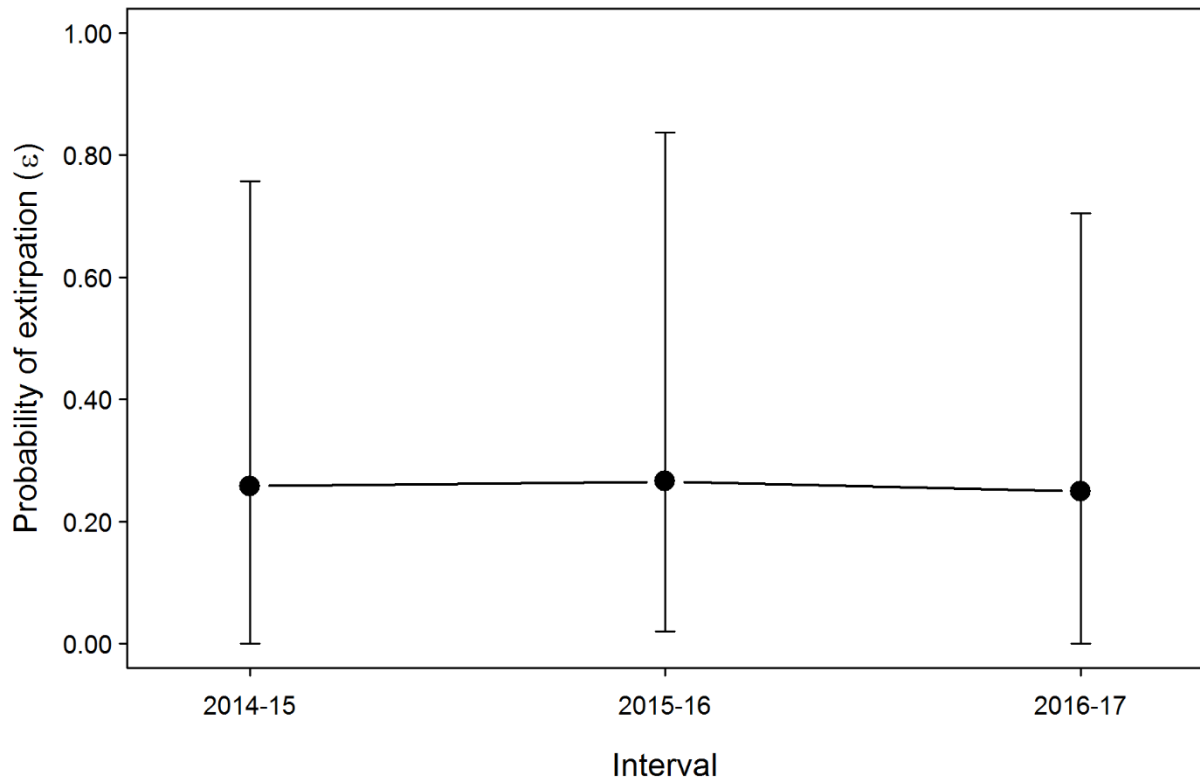


Figure 19. Graph showing annual mean probability of occupied arrays at one year being unoccupied the next year at Mindero Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

Effects of Habitat Diversity and Distance to Water on Probability of Extirpation

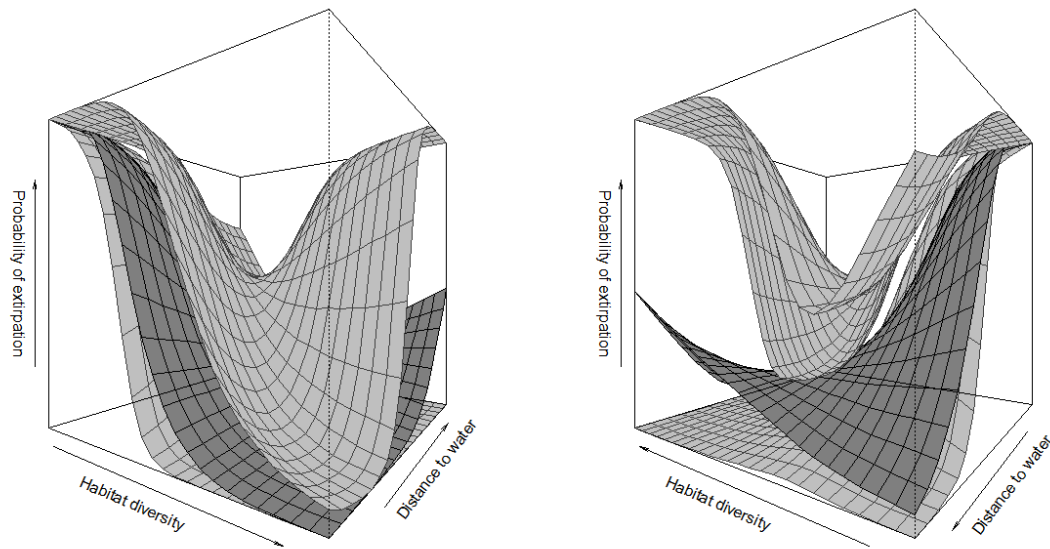


Figure 20. Model-averaged posterior distribution of the interaction between the effect of habitat diversity and the effect of distance to wetland on predicted probability of arrays occupied in one year being unoccupied the next year at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dark gray area indicates posterior median; light gray areas indicate 95-percent credible interval. Vector along each axis indicates increasing values for each variable.

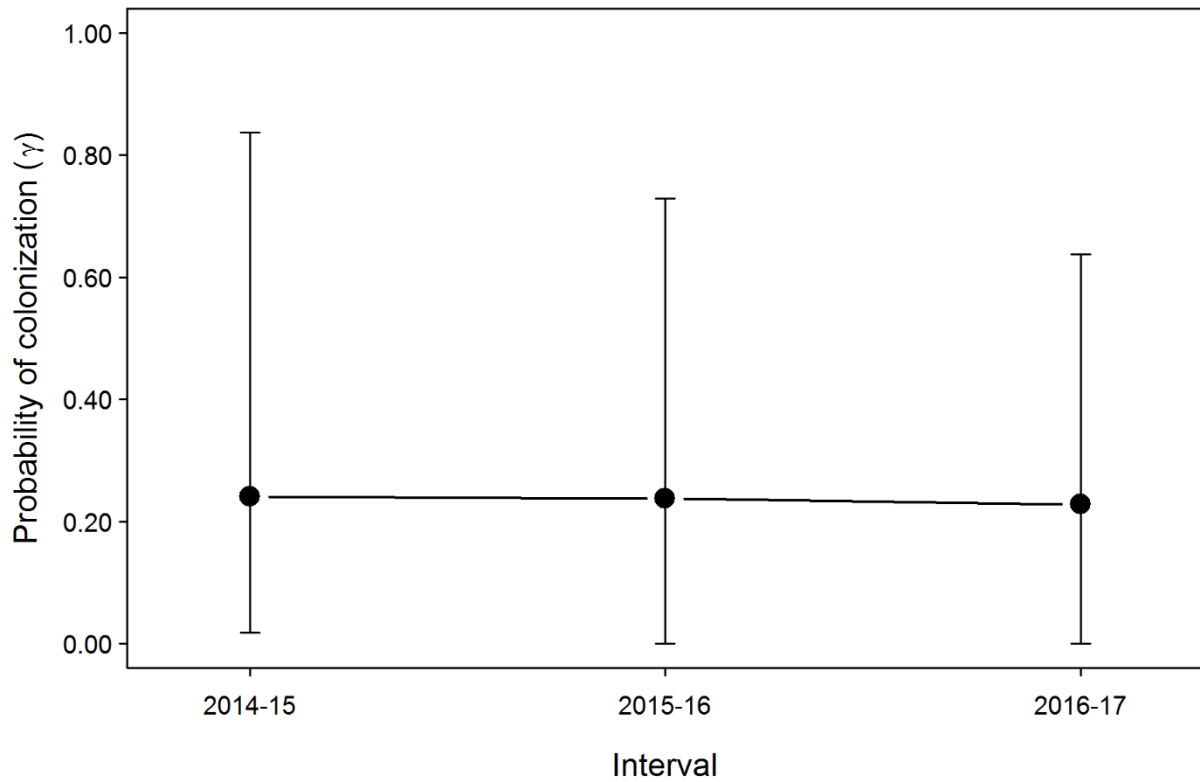


Figure 21. Graph showing annual mean probability of unoccupied arrays becoming occupied the next year at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

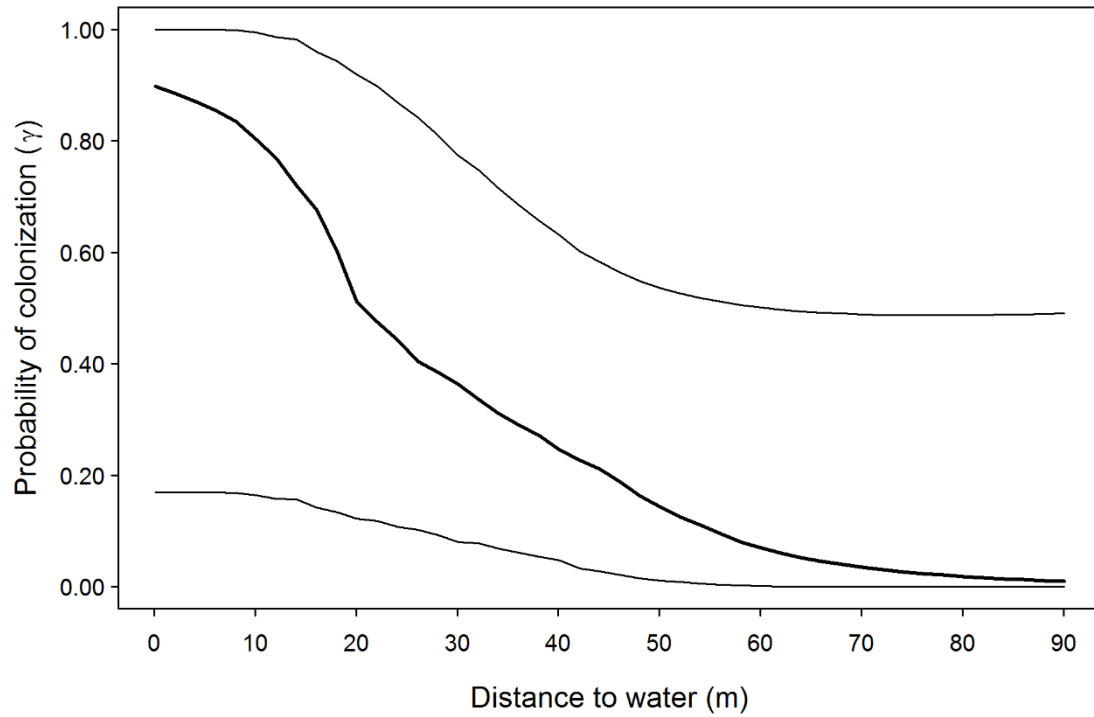


Figure 22. Graph showing effect of distance to wetland on probability of arrays unoccupied in one year being occupied the next year at Mindogo Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2015–17. Bold line indicates posterior mode; light lines indicate the 95-percent highest posterior density interval.

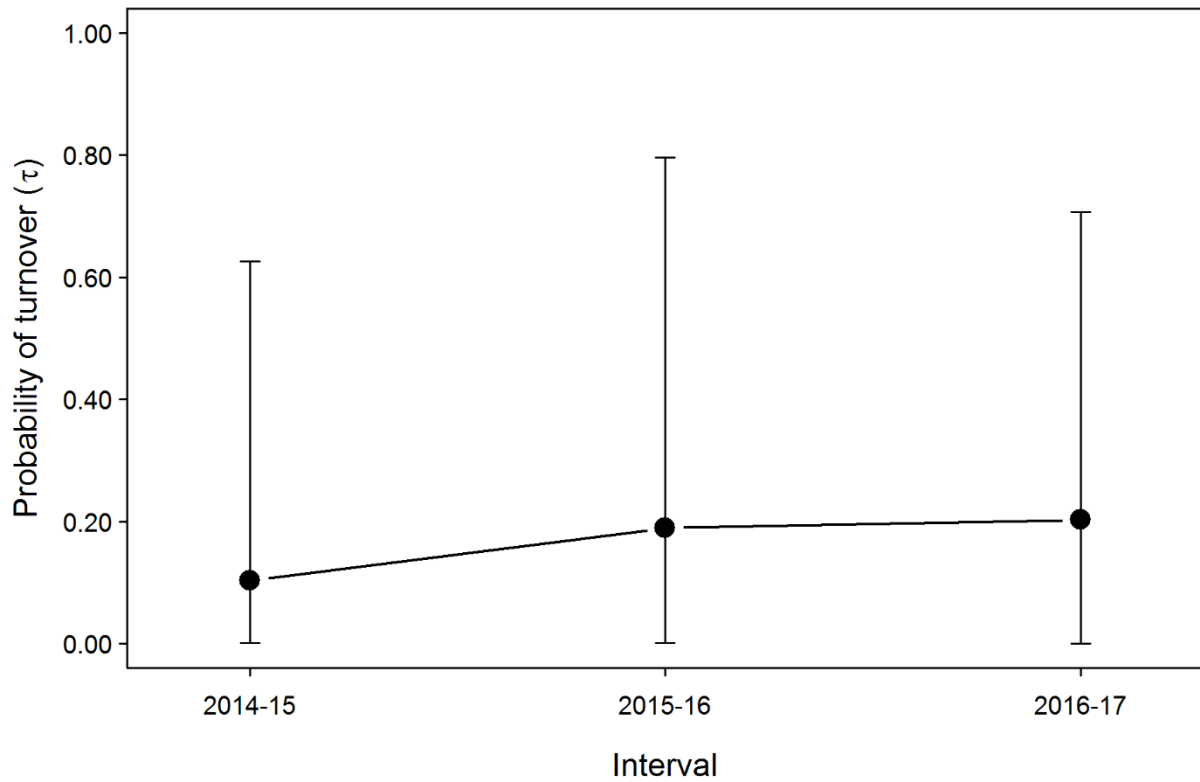


Figure 23. Graph showing annual probability that an occupied array in one year is a newly occupied one at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2015–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

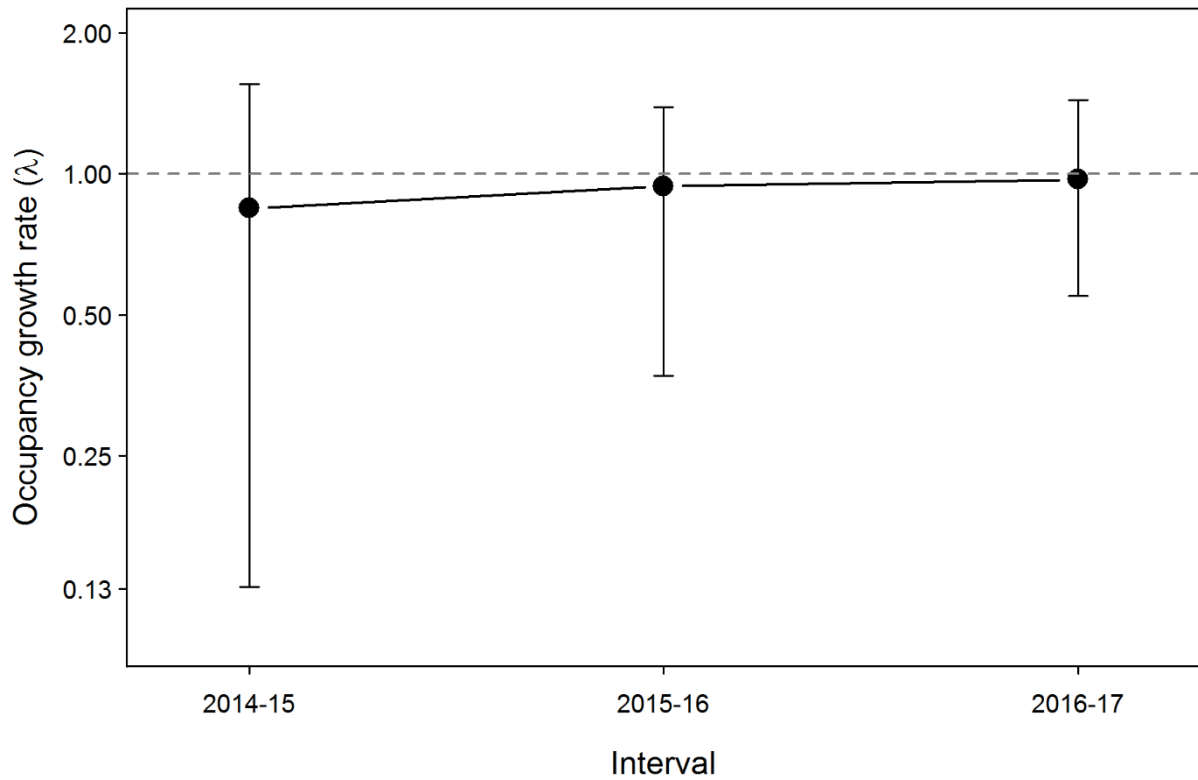


Figure 24. Graph showing annual occupancy growth rate of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindogo Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2015–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals; horizontal dashed line at 1 indicates a population in which occupancy is stable.

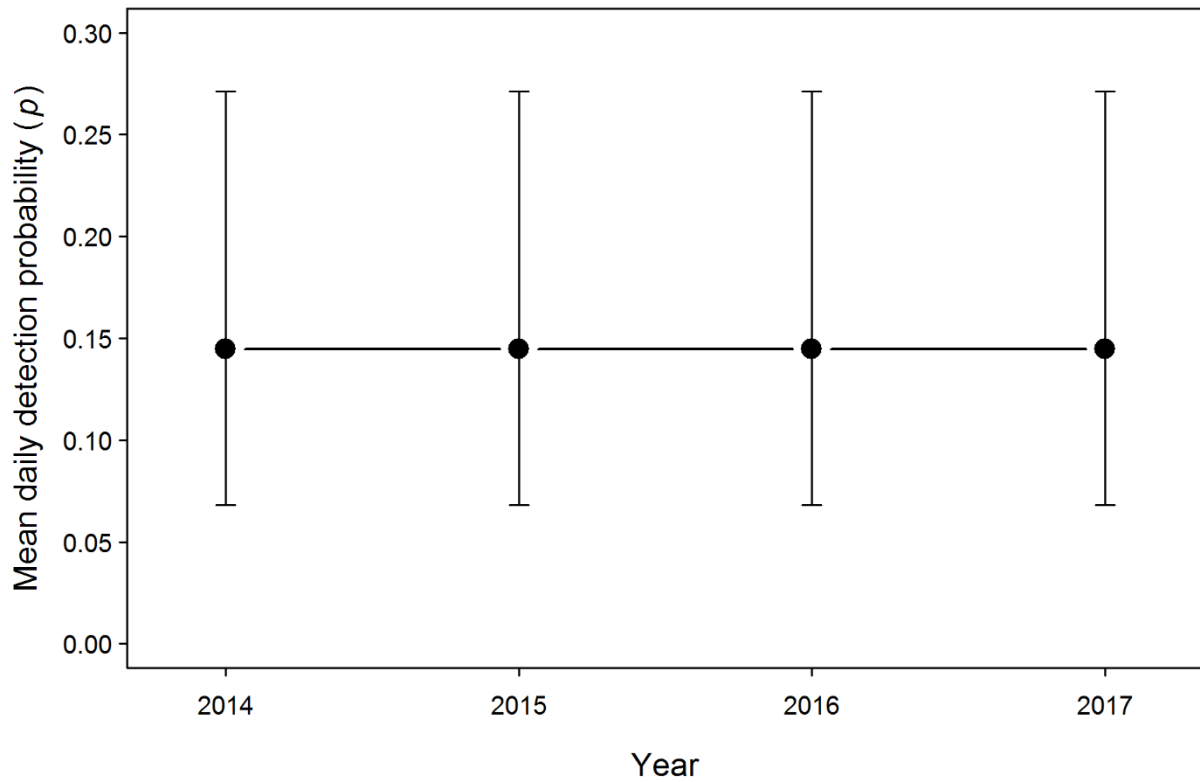


Figure 25. Graph showing annual daily detection probability of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

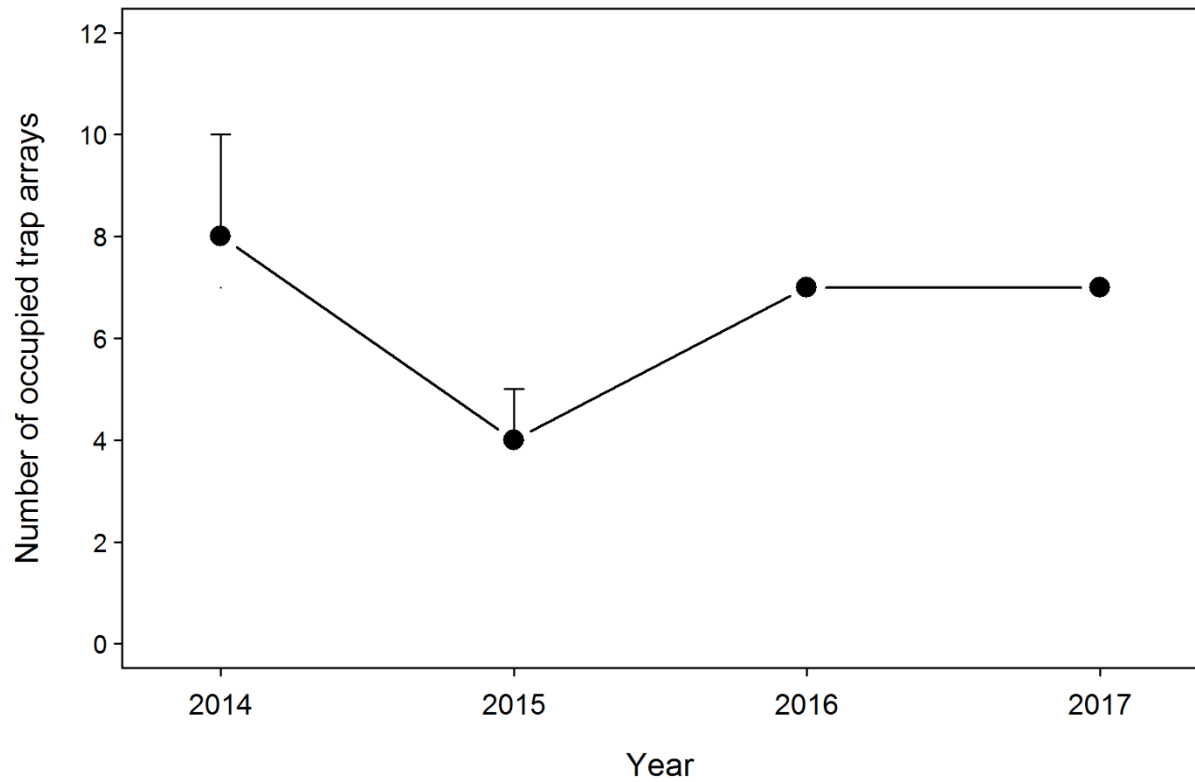


Figure 26. Graph showing model-estimated annual number of trap arrays occupied by San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals.

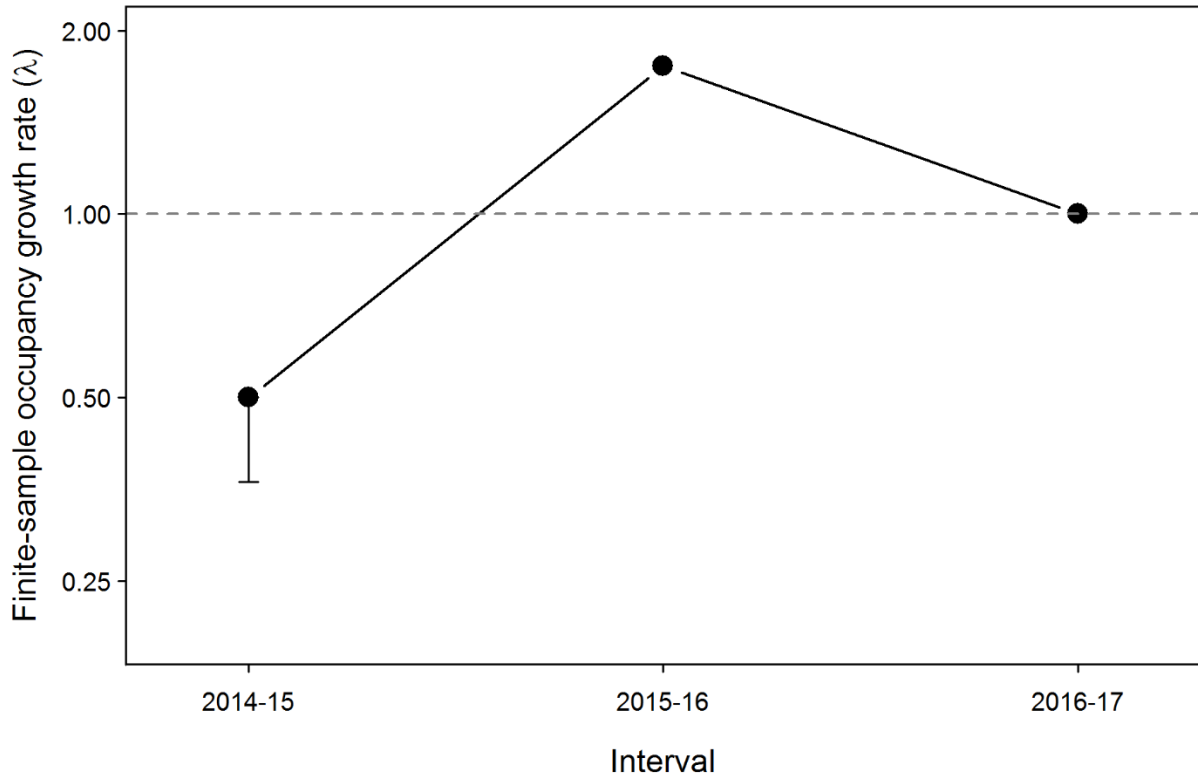


Figure 27. Graph showing annual finite-sample occupancy growth rate of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2015–17. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals. Horizontal dashed line at 1 indicates a population in which occupancy is stable.

Effect of Invasive Species Removal on San Francisco Gartersnakes and Native Anurans

The estimated probabilities of San Francisco gartersnake survival (ϕ), seniority (γ), recruitment (f), and population growth rate (λ) from the Pradel temporal symmetry model are summarized in table 16. Our results suggest that the reduction of apparent abundance of bullfrogs has a positive effect on the proportion of the San Francisco gartersnake population composed of new recruits ($1-\gamma$; fig. 28). Although 95-percent credible intervals included zero, the probability that reduced abundance of bullfrogs has a positive effect on recruitment of the snakes was 0.91 (fig. 29a), and the probability of having a positive effect on survival was 0.85 (fig. 29b). In accordance with higher seniority of San Francisco gartersnakes and with removal of bullfrogs in 2014, many more gravid female San Francisco gartersnakes were captured during 2015–17 than during 2014–15 (Figure 30), leading to lower seniority and higher recruitment in subsequent years. Based on the Pradel temporal symmetry model, the population growth rate of San Francisco gartersnakes was more likely to be stable or positive than negative, and was highest during 2015–17 (fig. 31).

Table 16. Posterior summaries of survival, seniority, recruitment, and population growth rate for the Pradel temporal symmetry model fitted to the San Francisco gartersnake population at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[Parameter estimates are presented as posterior mode (numbers in parentheses are 95-percent highest posterior density interval). **Symbols:** ϕ , survival; γ , seniority; f , recruitment; λ , population growth rate; >, greater than; <, less than; NA, not applicable]

Year	ϕ	γ	f	λ
2014	0.74 (0.48–>0.99)	NA	0.21 (<0.01–1.53)	1.07 (0.54–2.36)
2015	0.48 (0.30–0.80)	0.54 (0.30–>0.99)	0.84 (0.45–1.31)	1.35 (0.89–1.96)
2016	0.40 (0.19–0.81)	0.36 (0.24–0.53)	0.89 (0.40–1.72)	1.34 (0.70–2.39)
2017	NA	0.30 (0.19–0.47)	NA	NA

Apparent abundance of Sierran treefrogs, California red-legged frogs, and American bullfrogs quantified by egg mass counts and eye shine surveys are summarized in table 17 and figures 32–33. Bullfrogs were not detected in 2016 during the two eye shine surveys in April. Bullfrogs were not audibly detected in 2016 or 2017.

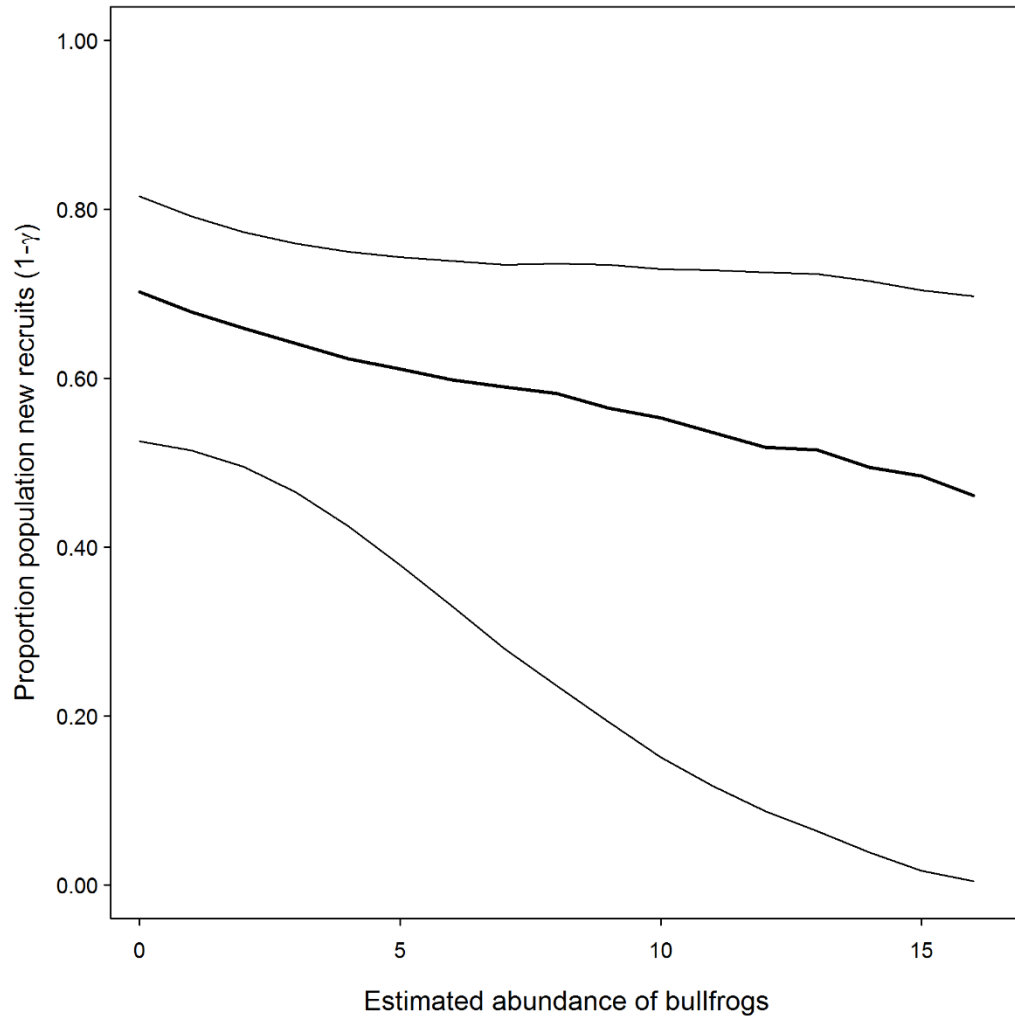


Figure 28. Graph showing posterior distribution of the effect of American bullfrog (*Lithobates catesbeianus*) abundance on mean recruitment of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Bold line indicates posterior mode; light lines indicate the 95-percent highest posterior density interval.

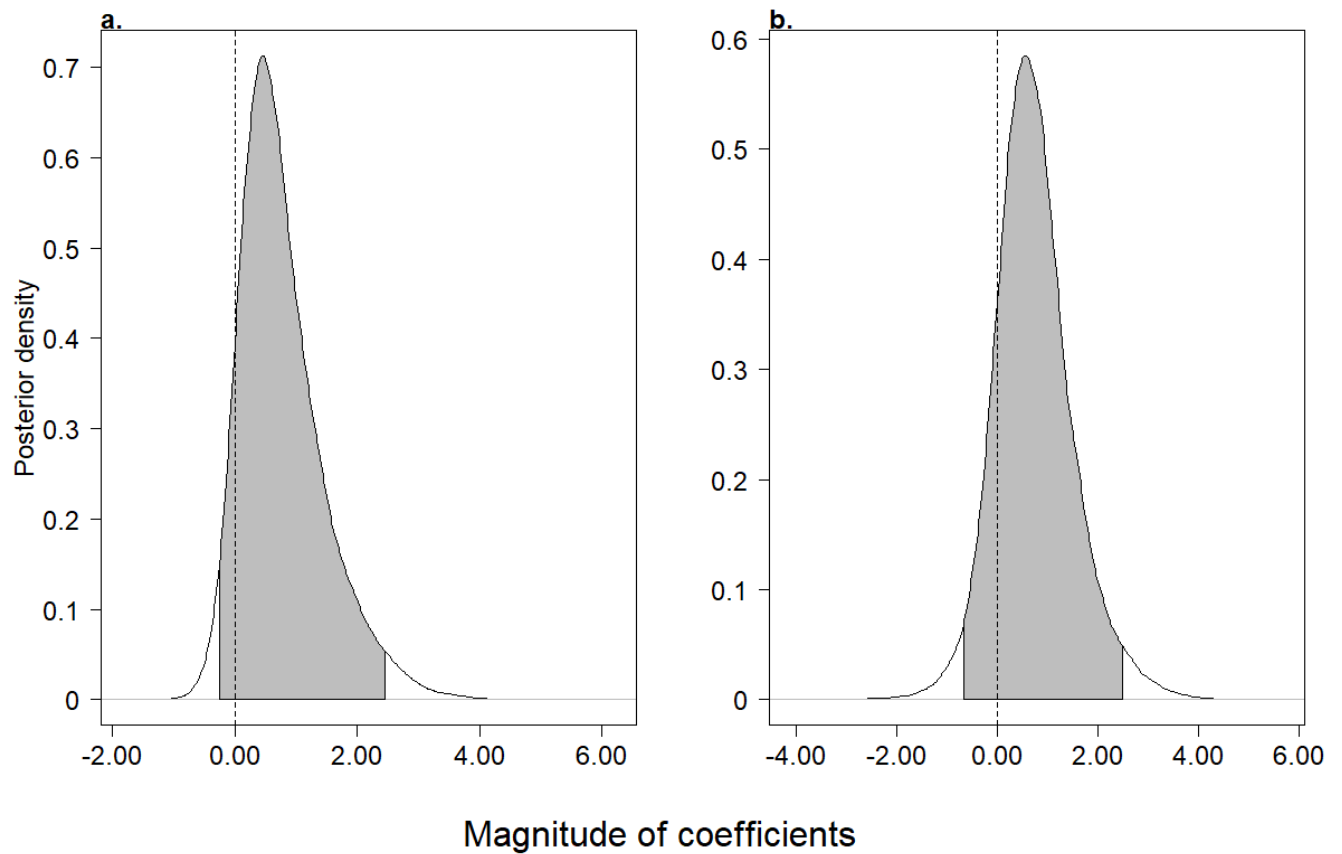


Figure 29. Graphs showing posterior distribution of the effect of bullfrog abundance on the seniority (a) and survival (b) of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindogo Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. Coefficients represent the change in the log-odds of seniority or survival with an increase of 8.5 bullfrogs. The shaded area represents the 95-percent posterior credible interval; dotted vertical lines represent no effect.

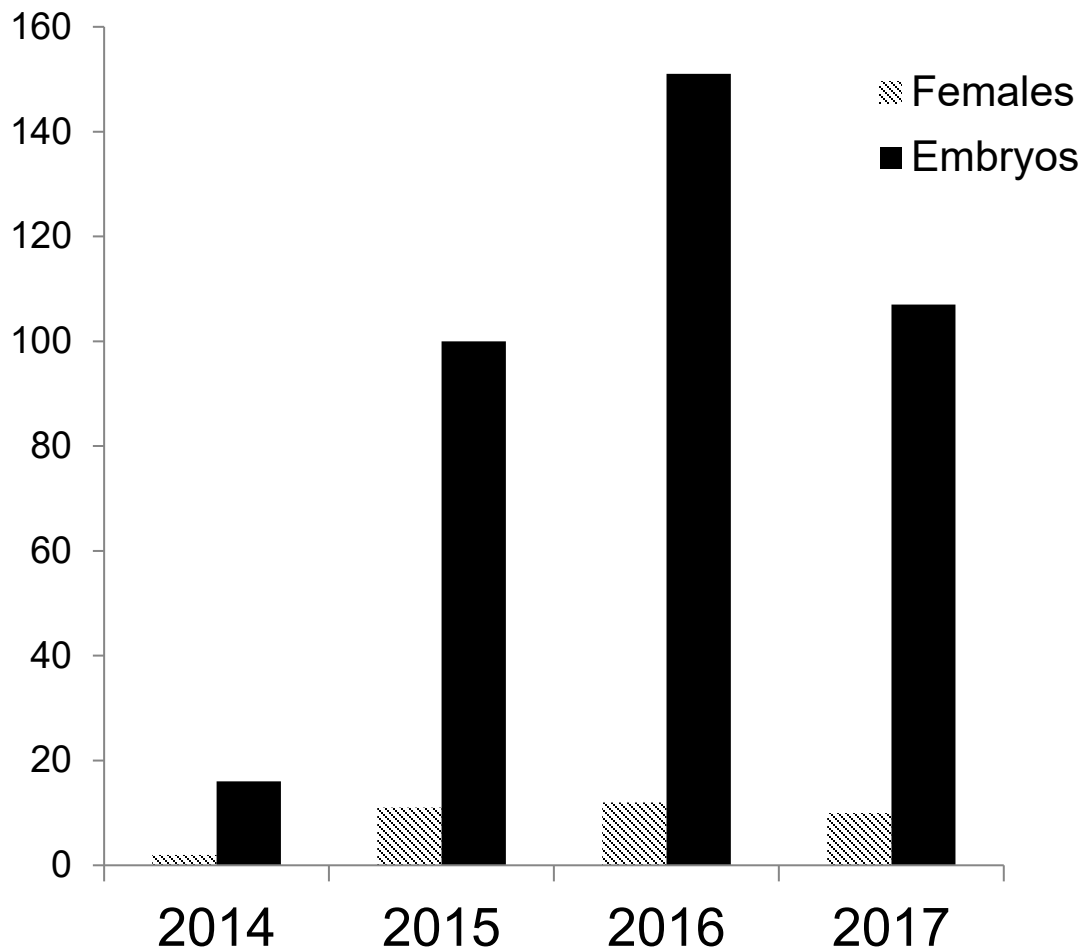


Figure 30. Graph showing total numbers of gravid females and minimum number of embryos identified by palpation each year at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17. True number of individual clutch size and successful birth rates for natural populations of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) are unknown.

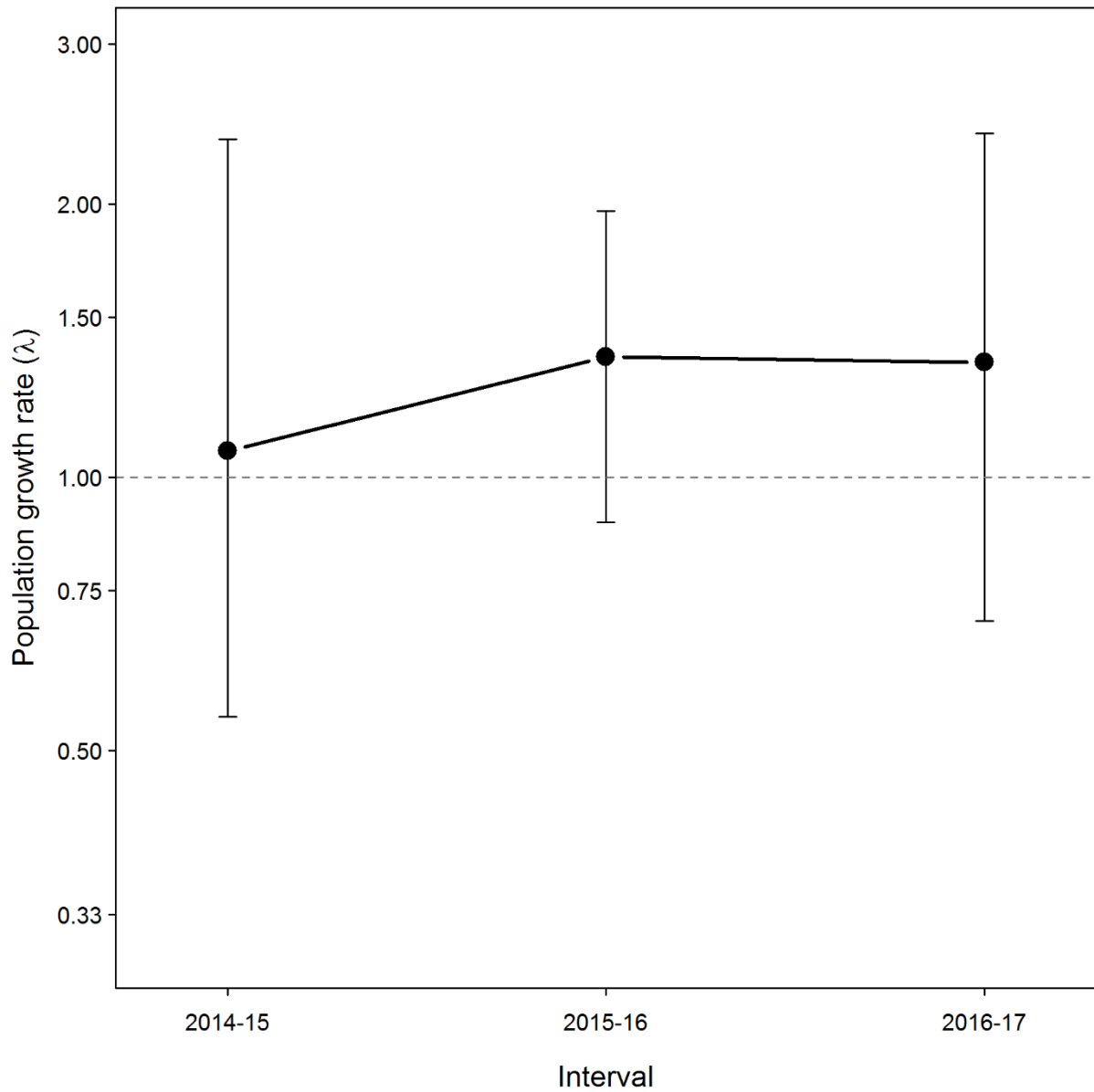


Figure 31. Graph showing annual population growth rate of San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17, based on the Pradel temporal symmetry model. Dots represent posterior modes; error bars represent 95-percent highest posterior density intervals. Horizontal dashed line at 1 indicates a stable population.

Table 17. Annual estimated abundance of anurans as available prey for San Francisco gartersnakes (*Thamnophis sirtalis tetrataenia*) and American bullfrogs (*Lithobates catesbeianus*) at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–15.

[Posterior mean and 95-percent credible intervals (in parentheses) of maximum number of estimated anurans are shown. Abundance of larval anurans was not quantified. Bullfrogs were not detected in 2016 during the two eye shine surveys in April. Bullfrogs were not audibly detected in 2016 nor 2017]

Year	Dates	Sierran treefrog (<i>Pseudacris sierra</i>)	California red- legged frog (<i>Rana draytonii</i>) adult	<i>Rana draytonii</i> metamorph	American bullfrog (<i>Lithobates</i> <i>catesbeianus</i>)
2014	April 5–13	5,405 (4,999–6,001)	1 (0–2)	0	16 (16–18)
	April 14–22	5,382 (4,992–5,859)	1 (0–2)	0	16 (16–18)
	April 23–May 21	5,375 (4,986–5,852)	1 (0–2)	0	16 (16–18)
2015	Feb 26–Mar 15	1,369 (962–1,775)	10 (6–15)	0	3 (3–5)
	April 1–9	1,395 (968–1,784)	10 (6–15)	0	3 (3–5)
	April 10–18	1,376 (1,008–1,822)	10 (6–15)	0	3 (3–5)
	April 19–27	1,415 (979–1,795)	10 (6–15)	0	3 (3–5)
	April 28–May 6	1,386 (991–1,807)	10 (6–15)	0	3 (3–5)
	May 7–24	1,408 (1,184–2,007)	10 (6–15)	0	3 (3–5)
	August 16–		10 (6–15)	21,880 (21,395–	3 (3–5)
	September 18	223 (222–223)		24,327)	

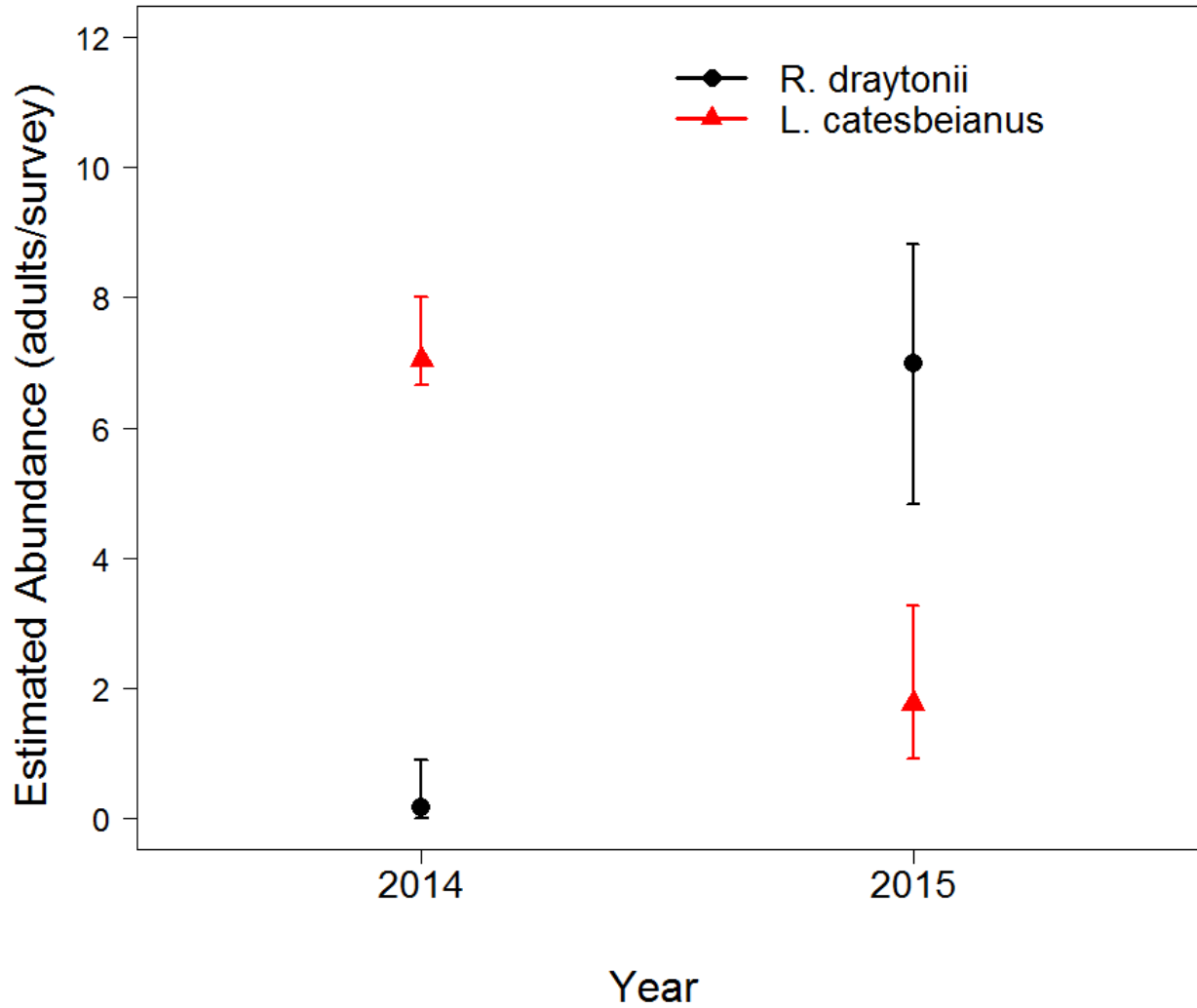


Figure 32. Graph showing average abundance of adult California red-legged frogs (*Rana draytonii*) and American bullfrogs (*Lithobates catesbeianus*) estimated by nocturnal eye shine surveys at Aquatic Feature 3 at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–15. Dots represent posterior means; error bars represent 95-percent credible intervals. Bullfrogs were not detected in 2016 during the two eye shine surveys in April. Bullfrogs were not audibly detected in 2016 and 2017.

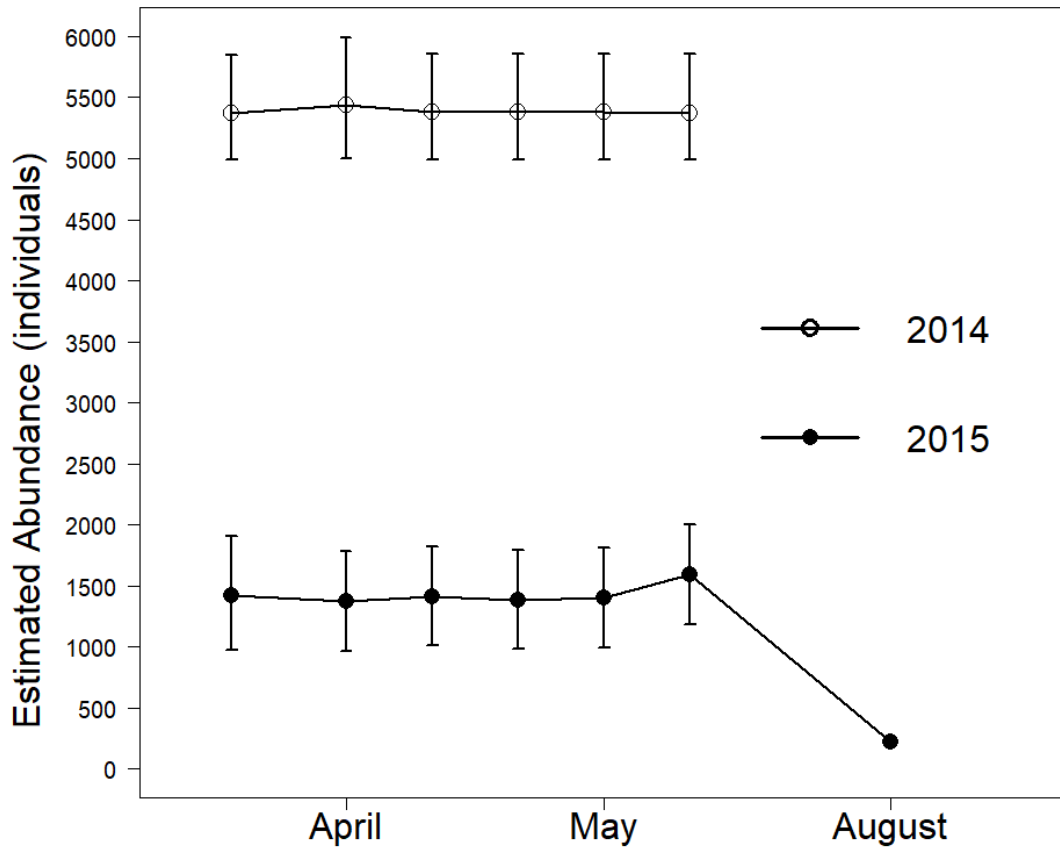


Figure 33. Average abundance of adult and metamorphosed Sierran treefrogs (*Pseudacris sierra*) estimated by egg mass counts and trap bycatch at Aquatic Feature 3 at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–15. Dots represent posterior means; error bars represent 95-percent credible intervals.

Other Vertebrate Trap Contents

In addition to San Francisco gartersnakes, we captured and marked 226 coast gartersnakes, 41 Santa Cruz gartersnakes, 72 Pacific gophersnakes, 5 rubber boas, 203 western yellow-bellied racers, 3 Pacific ring-necked snakes, and 5 sharp-tailed snakes in funnel traps, indicating a diverse and abundant snake community at Mindego Ranch (tables 18–19).

Table 18. Total numbers of vertebrate captures by trap array at Mindogo Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[Numbers do not represent individually marked animals]

Common name	Scientific name	Trap Array											
		A	B	C	D	E	F	G	H	I	J	K	L
Western yellow-bellied racer	<i>Coluber mormon</i>	15	13	18	16	54	59	10	6	3	13	11	27
Sharp-tailed snake	<i>Contia tenuis</i>	0	0	4	1	0	0	0	0	0	0	0	0
Pacific ring-necked snake	<i>Diadophis punctatus amabilis</i>	0	0	0	0	0	1	1	1	0	0	0	0
Pacific gophersnake	<i>Pituophis catenifer catenifer</i>	0	1	2	4	13	15	2	14	5	13	3	2
Rubber boa	<i>Charina bottae</i>	0	0	0	0	0	0	1	0	0	0	0	0
Santa Cruz gartersnake	<i>Thamnophis atratus atratus</i>	0	0	1	7	0	0	2	7	0	0	14	0
Coast gartersnake	<i>Thamnophis elegans terrestris</i>	32	8	56	65	42	16	13	21	0	3	8	4
Northern alligator lizard	<i>Elgaria coerulea</i>	0	2	0	0	0	3	2	3	2	0	0	3
Southern alligator lizard	<i>Elgaria multicarinata</i>	0	3	0	0	5	4	4	3	0	3	0	1
Western fence lizard	<i>Sceloporus occidentalis</i>	1	0	4	2	14	1	7	3	2	0	1	2
Sierran treefrog	<i>Pseudacris sierra</i>	7	33	246	139	28	27	23	5	0	6	111	21
Yellow-eyed ensatina	<i>Ensatina eschscholtzii xanthoptica</i>	2	1	0	0	0	0	2	1	0	0	0	0
Pacific newt	<i>Taricha</i> sp.	1	3	0	0	0	2	0	1	3	0	13	33
Deer mouse	<i>Peromyscus</i> sp.	22	7	9	14	13	4	4	14	6	5	4	5
Vole	<i>Microtus</i> sp.	12	10	12	9	3	4	2	3	1	0	1	1
Dusky-footed woodrat	<i>Neotoma fuscipes</i>	0	0	0	0	0	0	1	0	0	0	0	0
Long-tailed weasel	<i>Mustela frenata</i>	0	0	0	0	0	0	0	1	0	0	0	0

Table 19. Total numbers of vertebrate captures in traps, precipitation, and mean temperature by year at Mindego Ranch, Russian Ridge Open Space Preserve, San Mateo County, California, 2014–17.

[Weather data are for the water year (October 1 of preceding calendar year to September 30), with year indicating the calendar year at the end of the water year. Precipitation and temperature data were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information, Station USC00048273, accessed February 20, 2018, at <https://www.ncdc.noaa.gov/cdo-web/>]

Common name	Scientific name	Year			
		2014	2015	2016	2017
Western yellow-bellied racer	<i>Coluber mormon</i>	99	78	51	17
Sharp-tailed snake	<i>Contia tenuis</i>	3	1	1	0
Pacific ring-necked snake	<i>Diadophis punctatus amabilis</i>	0	1	0	2
Pacific gophersnake	<i>Pituophis catenifer catenifer</i>	21	25	24	4
Rubber boa	<i>Charina bottae</i>	1	0	0	0
San Francisco gartersnake	<i>Thamnophis sirtalis tetrataenia</i>	34	31	108	110
Santa Cruz gartersnake	<i>Thamnophis atratus atratus</i>	9	8	10	4
Coast gartersnake	<i>Thamnophis elegans terrestris</i>	69	62	81	56
Northern alligator lizard	<i>Elgaria coerulea</i>	0	4	9	2
Southern alligator lizard	<i>Elgaria multicaerulea</i>	1	11	6	5
Western fence lizard	<i>Sceloporus occidentalis</i>	8	21	2	6
Sierran treefrog	<i>Pseudacris sierra</i>	25	331	113	177
Yellow-eyed ensatina	<i>Ensatina eschscholtzii xanthoptica</i>	0	3	3	0
Pacific newt	<i>Taricha</i> sp.	0	23	26	7
Deer mouse	<i>Peromyscus</i> sp.	27	61	11	8
Vole	<i>Microtus</i> sp.	0	48	10	0
Dusky-footed woodrat	<i>Neotoma fuscipes</i>	0	0	1	0
Long-tailed weasel	<i>Mustela frenata</i>	0	0	1	0
Weather data					
Annual precipitation (in millimeters)		513	883	1,210	1,577
Mean annual temperature (in degrees Celsius)		15.2	15.2	14.7	14.3

Discussion

San Francisco gartersnakes are moderately abundant at Mindego Ranch. The estimated abundance based on the open Jolly-Seber model suggests that the population currently (2018) is stable, with about 100–150 individuals in the sampled area at the site. Abundance peaked in 2016, with relatively high survival and the highest recruitment and population growth rates in the interval between 2015 and 2016. Apparent survival decreased between 2016 and 2017, but the estimated population size remained higher in 2017 than in 2014 and 2015, and recruitment in 2017 was still higher than in 2015. The underlying cause of the decrease in apparent survival remains obscure, but an overall interpretation of recruitment, survival, and size distributions could indicate that the population has experienced a “turnover” of more recruitment of new individuals and more mortality of older individuals in 2016 and 2017 compared to 2014 and 2015. For example, annual distributions of SVL provide evidence that female populations in 2016 and 2017 consist of smaller and younger individuals than those in 2014 and 2015. Compared to previous years, in 2017 we sampled a greater proportion of the annual true population and also the highest number of individual females (31 individuals); therefore, it is unlikely that the finding of a lack of older females (>700 mm SVL) in 2017 was caused by insufficient sampling. The lower estimated abundance in 2017 and population growth rate between 2016 and 2017, compared to the year before, could indicate that the mortality rates of older individuals were higher in 2016. The overall increase in per-capita recruitment from 2015 to 2016 and 2017 aligns with our anecdotal observations of neonates. Many neonatal and young-of-the-year San Francisco gartersnakes were observed near Aquatic Feature 3 in the late summer of 2015 and 2016. We also observed more gravid females and detected a larger total number of embryos in 2015–17 compared to 2014.

Our results suggest that increased precipitation and extirpation of invasive species at Aquatic Feature 3 positively influenced the recruitment of San Francisco gartersnakes. Recruitment probabilities in 2016 and 2017 were higher, and seniority parameters were lower, than in 2015, likely following the recruitment of native anurans in 2015. Increased precipitation likely sustained the anuran populations until autumn, allowing abundant prey for young San Francisco gartersnakes. However, we did not find strong evidence that prey abundance affected apparent survival. Apparent survival probability of San Francisco gartersnakes in 2016 was lower than in 2014, when recruitment of anurans did not occur. Our results showed increased availability of California red-legged frogs and metamorphosed Sierran treefrogs after the drying of Aquatic Feature 3 and reduction of American bullfrogs in 2014. Therefore, the apparent survival probability of San Francisco gartersnakes in 2016 might have been limited by sources other than prey availability (Reeder and others, 2015), such as predation, environmental constraints, and demographic stochasticity, which can have large effects on relatively small populations (Lande, 1993). Comparable observations were made from capture histories of congeners; the capture rates of coast gartersnakes and Santa Cruz gartersnakes also increased between 2014 and 2016 but decreased in 2017 (table 19), likely showing a decrease in apparent survival probabilities in 2016 similar to San Francisco gartersnakes. Although interesting, a more thorough CMR analysis of these species is beyond the scope of this report.

The increased apparent abundance of metamorphosing and adult California red-legged frogs in 2015 directly indicates abundant prey availability for large San Francisco gartersnakes during that same year, as the snakes select California red-legged frogs over American bullfrogs, and consumption of California red-legged frogs increased in 2015 (Kim, 2017). Although we did not conduct extensive amphibian abundance surveys in 2016 and 2017, we visually identified metamorphosed California red-legged frogs and many adult California red-legged frogs at Aquatic Feature 3 in spring of both years.

The effect of grazing on San Francisco gartersnake distribution or demography could not be quantified by our study. We could not assess the effect of grazing as a binomial “treatment” variable because of the small number of trap arrays and lack of control arrays, which must be isolated from grazing during the entire study period. Nonetheless, our results highlighted that maintaining habitat diversity, particularly near wetlands, reduces the probability of local extirpation. Therefore, San Francisco gartersnakes might benefit from low-intensity cattle grazing, as long as it promotes habitat heterogeneity in and near wetlands. Our results also highlighted that regardless of the level of habitat diversity, proximity to water increases local colonization of arrays by San Francisco gartersnakes. This likely is following the phenology and spatial distribution of amphibian prey. Therefore, limiting cattle disturbance to emergent shoreline vegetation during amphibian breeding (February–March) and metamorphosis (July–August) likely would maintain a large prey base for the snakes, as well as prevent direct mortality of foraging snakes by cattle trampling.

Results from the closed population model largely agreed with those of the Jolly-Seber model, except that abundance was estimated with less certainty in the closed model. Based on the closed model, the probability that abundance in the sampled area was greater than the target of 200 individuals in the Recovery Plan for the San Francisco Garter Snake (U.S. Fish and Wildlife Service, 1985) was 0.07 in 2014, 0.24 in 2015, 0.60 in 2016, and 0.01 in 2017. The reason for the decrease following 2016 is uncertain, as is whether this is a biologically meaningful decrease or within the bounds of normal annual variation at Mindego Ranch. Regardless of the situation, the within-season recapture rate was the highest in 2017 (five individuals recaptured four times and eight individuals recaptured three times); therefore, the true population size was estimated with the highest precision in 2017. The apparent reduction in abundance from 2016 to 2017, therefore, might have been caused, in part, by lower capture probabilities, which led to higher uncertainty and a higher abundance estimate in 2016. When comparing abundance across years, open population models likely are more reliable, as they account for recaptures of individuals in different years.

The relatively stable abundance of San Francisco gartersnakes in time is in contrast to their heterogeneous spatial distribution. Although some San Francisco gartersnake captures occurred in trap arrays or cover objects associated with each water body, most snakes were associated with Aquatic Feature 3, especially on the east side near arrays C and D. This concentration of San Francisco gartersnakes around Aquatic Feature 3 was especially evident in the early years of the study that coincided with drought in California. Habitat diversity was positively related to persistence of San Francisco gartersnakes at traps and to localized relative San Francisco gartersnake abundance in 2014, but not in other years. In these latter years of the study, the distribution of San Francisco gartersnakes was less concentrated on a single array than earlier in the study. Increased abundance and a broader distribution of anuran prey likely was related to increased annual precipitation that promoted amphibian reproduction at other water bodies and facilitated amphibian dispersal across the landscape. The greater availability of prey,

both in absolute terms and in their spatial distribution, and increased humidity likely allowed dispersal of snakes away from their drought refugia. Despite the decrease in their true population as estimated by closed population and Jolly-Seber models, the distribution of San Francisco gartersnakes was wider in 2017 than in previous years. Because CMR models cannot distinguish between permanent emigration and mortality, lower abundance estimates in 2017 and low apparent survival in 2016–17 possibly were the result of San Francisco gartersnakes being less concentrated near water bodies, where sampling was most intensive, in the wettest final year of the study. High capture probabilities in 2017, however, might be evidence contrary to this hypothesis.

The increased probabilities of occurrence and increased number of trap arrays occupied since 2015 could be described by the probabilities of local extirpation and colonization. Increased habitat diversity since 2015, from increased precipitation (table 19), could have encouraged San Francisco gartersnakes to remain at the array the following year, and local colonization rates did not decrease throughout the study. Arrays closer to wetlands were more likely to be colonized, potentially because of higher amphibian prey availability or more favorable environmental conditions. The turnover probability supported results of the spatial distribution analysis; snakes were not concentrated at one or two trap arrays in 2016 and 2017, which aligns with the overall higher probabilities that an occupied array in these years had been colonized during the preceding interval.

The most prominent result following increased precipitation and removal of invasive fish and American bullfrogs at Mindego Ranch was the population-level response of native anurans. Increase in the apparent abundance of California red-legged frogs and Sierran treefrogs, which serve as prey for San Francisco gartersnakes, might have been caused by the removal of invasive predators, increased hydroperiods associated with greater rainfall in 2015 and 2016, or both. The increased number of adult California red-legged frogs in 2015 likely is not caused by recruitment from 2014, but instead is caused by a shift in behavior of existing adults in the absence of the fish and bullfrogs (D'Amore and others 2009). Our egg mass surveys provided an index of the relative change in the abundance of Sierran treefrogs and Pacific newt species at Aquatic Features 2 and 3 before and after removal of invasive species. The decrease in Sierran treefrog egg mass counts from 2014 to 2015 might be related to changes in breeding habitat. In 2014, Sierran treefrogs oviposited in mud crevices at the bottom of the lake, where water was relatively shallow with minimal vegetation obstructing the vision of observers. In 2015, it was harder to detect egg masses because the water level was higher and the observer vision was obstructed by dense floating and submerged vegetation.

The size distributions and sex ratios of San Francisco gartersnakes at Mindego Ranch were consistent with a healthy snake population. San Francisco gartersnakes of both sexes in a range of sizes were captured, likely indicating a population with a diverse age structure. Sexual size dimorphism, with females representing the larger sex, was evident at Mindego Ranch, although sexual size dimorphism in SVL was not statistically significant. Mean female SVL in 2017 was the shortest among all years and also smaller than male SVL. Although this could be caused by increased mortality of older snakes, it also is possible that large females might have used different parts of Mindego Ranch, whereas in 2014 and 2015 their activities were more restricted to the upland-riparian corridor near Array D. Because of the increased water level from the previous winter, we were not able to access the southern perimeter of Aquatic Feature 3 and hand-capture any individuals in 2017. Some large females initially captured in arrays C or D in 2014 and 2015 were recaptured by hand in 2016 on the southern perimeter of Aquatic Feature 3.

Although the sex ratio of San Francisco gartersnakes at Mindego Ranch was slightly male-biased, we do not expect that sex ratios are extreme enough to limit population growth. We included an assessment of sex ratio in the CMR model, and compared bias-corrected sex ratios to the naïve sex ratios calculated using a simple binomial model. If sex does not affect capture probability, then naïve sex ratios should be a good estimate of true sex ratios that account for differences in capture probabilities. Thus, the agreement of the two results in 2014 and 2017 likely was because little evidence existed for an effect of sex on capture probability.

San Francisco gartersnake capture probabilities were affected by several environmental variables. Throughout our study, a positive ephemeral behavioral response, random daily variation, a positive effect of air temperature, and, in some years, sex affected capture probabilities of San Francisco gartersnakes. A positive behavioral response could have been caused by trap-happiness, whereby snakes were rewarded with an easy-to-capture meal when they entered a trap, by their continued proximity to trap arrays while foraging following release, or by behavioral patterns, such as foraging bouts lasting multiple days followed by retreat to refugia for digestion or shedding. Short-term positive behavioral responses to capture are not unusual in CMR studies of gartersnakes that use passive sampling (Brian Halstead, U.S. Geological Survey, personal observation). Unexplained temporal heterogeneity in San Francisco gartersnake capture probabilities likely was caused by unmeasured variables, such as insolation, by specific combinations of variables (for example, warm days following rain events), or by unmeasurable behavioral patterns in snakes.

Snakes are notoriously difficult to detect (Durso and others, 2011), and low San Francisco gartersnake capture probabilities limited some aspects of our results. For example, because capture histories were sparse and capture probabilities low, we could not conduct a separate CMR analysis of abundance for each water body. Furthermore, the long-distance movement of some individuals between water bodies suggests that populations are not closed to movement between water bodies during our sampling period, and suggests that separately modelling abundance at each water body would be inappropriate.

Deploying cover objects increased the capture rate and detection of San Francisco gartersnakes. Ten percent of captures between 2015 and 2017 were under cover objects. At Aquatic Feature 2, San Francisco gartersnakes were captured more frequently under cover objects than in trap arrays. Future monitoring of the San Francisco gartersnake population at Mindego Ranch could be continued by redeploying cover objects. Cover objects have the advantage over traps of being cheaper and easier to deploy, and they do not need to be checked regularly because individuals are not detained in them. The primary drawbacks to cover objects are that animals sheltering under them can be crushed if cattle, humans, or other large animals step on them, and they function most effectively when they have “seasoned” for at least a winter. Therefore, grazing can make cover objects less suitable or effective for monitoring. Cover objects also are not suitable where poaching is a concern.

As an alternative to cover objects, visual surveys for San Francisco gartersnakes also could be used for monitoring. Visual surveys are highly sensitive to site and survey conditions (insolation, air temperature, season, and vegetation density), so we do not recommend visual surveys for estimating abundance. Nonetheless, repeated visual surveys during warm days in early spring (March–April) might be effective for confirming that San Francisco gartersnakes continue to occur at the site.

The San Francisco gartersnake population at Mindego Ranch is stable and numbers in the hundreds of individuals. Maintaining habitat heterogeneity at small spatial scales, especially close to wetlands, should benefit these rare snakes. Increasing the abundance of anuran prey also would likely benefit San Francisco gartersnakes; management actions to eliminate or reduce the abundance of invasive aquatic vertebrates likely improved site conditions for both native amphibians and San Francisco gartersnakes at the site. Continued management of non-native predators and habitat likely would maintain the San Francisco population at Mindego Ranch well into the future, and long-term monitoring of San Francisco gartersnakes could continue to assess any potential changes in population status.

Summary

Based on the results of this study, we conclude that:

- San Francisco gartersnake populations at Mindego Ranch, San Mateo County, California, likely were stable or increasing from 2014 to 2017.
- Apparent survival was relatively high, except during 2016–17. Low apparent survival in this interval was offset by high recruitment rates, especially of small snakes.
- Sex ratios and size distributions of San Francisco gartersnakes at Mindego Ranch were consistent with healthy snake populations.
- Small-scale (within 25 meters) habitat heterogeneity was positively associated with occurrence and abundance of San Francisco gartersnakes at trap arrays, and also was positively related to the probability that snakes would persist at these arrays.
- The effects of drought and management cannot readily be separated in our analysis; nonetheless, removal of non-native fish and culling of bullfrogs were correlated with increases in native anuran and San Francisco gartersnake abundance and recruitment.
- The effect of grazing on San Francisco gartersnake distribution or demography could not be quantified by our study. To the extent that low-intensity grazing promotes habitat heterogeneity (particularly shrubby grasslands near wetlands, ponds, and lakes), San Francisco gartersnakes should benefit.
- Installing cattle exclusion fences in subsections of Aquatic Features 2 and 3 and adjacent uplands could protect the breeding habitat of California red-legged frogs and Sierran treefrogs and also increase the survival of their metamorphs to benefit both native anurans and San Francisco gartersnakes.
- Sampling with cover objects was effective in detecting and increasing captures of San Francisco gartersnakes, especially at Aquatic Feature 2. In the absence of trap arrays, cover objects would be the most reliable and cost-effective method of sampling San Francisco gartersnakes, provided that crushing of snakes and poaching could be avoided.
- A long-term monitoring program for San Francisco gartersnakes is important for detection of population change and the variables related to any changes, and likely would contribute to early detection of population decreases and prevention of extirpation from Mindego Ranch.

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