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International System of Units to Inch/Pound

Multiply	By	To obtain
Length		
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
Area		
square kilometer (km^2)	247.1	acre
square kilometer (km^2)	0.3861	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.

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Introduction

Background

The California Department of Water Resources (DWR) manages the State's water resources in collaboration with other parties. In fulfilling this role, DWR supports efforts that promote water-supply reliability. The 2009 Water Plan identifies water transfers as one of the resource management areas to assist in achieving water-supply reliability. Water transfers involve the temporary, long-term, or permanent transfer of water rights from willing sellers to willing buyers. One of the mechanisms by which water is made available for transfer is by idling a crop and transferring the crop's consumptive water use. Rice from the Sacramento Valley is by far the most common crop that is idled for the purpose of water transfers. The transfers of water made available by idling rice can deplete water resources necessary for plants and wildlife that use rice fields as habitat, particularly aquatic and wetland-dependent species.

Giant gartersnakes (*Thamnophis gigas*) comprise an obligate wetland species endemic to marshes and marsh-like habitats in the Central Valley of California. Because of the loss of nearly all their native tule (*Schoenoplectus* spp.) marsh habitat, giant gartersnakes are listed under the Federal and State endangered species acts as threatened (California Department of Fish and Game Commission, 1971; U.S. Fish and Wildlife Service, 1993). Although they are now extirpated from most of the southern part of their former range, giant gartersnakes persist in the Sacramento Valley in remnant marshes and sloughs and rice-growing agricultural habitats (Halstead and others, 2010).

Although the distribution of habitats suitable for giant gartersnakes in the Sacramento Valley has been examined (Halstead and others, 2010), the distribution of giant gartersnakes in the Sacramento Valley and the variables affecting this distribution are not well known. Knowledge of the variables affecting the distribution of giant gartersnakes will assist resource managers in the conservation and recovery of the species by avoiding actions that could result in the take (disturbance, injury, or mortality) of giant gartersnakes or damage to their habitat in areas where they are most likely to occur.

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Goals and Objectives

The primary objectives of this project were to examine the distribution of giant gartersnakes in regions of rice agriculture in the Sacramento Valley, and to quantify variables—such as landscape-level habitat, local microhabitat, vegetation composition, and prey counts—associated with the occurrence of giant gartersnakes. This objective is an important early step for the goal of establishing a long-term programmatic assessment of the relation of giant gartersnakes with rice agriculture and other habitats in the Sacramento Valley. In particular, it provides information on where giant gartersnakes occur and are likely to occur, which has value for managing water transfers to minimize effects on giant gartersnakes.

Biology of Giant Gartersnakes

Giant gartersnakes are precinctive to wetlands in California's Central Valley. They were first described in the southern San Joaquin Valley by Fitch (1940) as a subspecies of aquatic gartersnakes (at that time, *Thamnophis ordinoides*). Further taxonomic revisions resulted in the consideration of giant gartersnakes as a subspecies of sierra gartersnakes (*Thamnophis couchii*). Because giant gartersnakes are morphologically distinguishable from and do not occur at the same locations as their most closely related species, aquatic gartersnakes (*Thamnophis atratus*) and sierra gartersnakes, they were recognized as a full species in 1987 (Rossman and Stewart, 1987).

Giant gartersnakes are highly aquatic and historically occurred in marshes, sloughs, and other habitats with slow-moving, relatively warm water and emergent vegetation, especially tules (*Schoenoplectus* [*Scirpus*] *acutus*). Although conversion of wetlands to agriculture has nearly extirpated giant gartersnakes from the San Joaquin Valley, this species persists in remnant marshes and sloughs and rice agriculture in the Sacramento Valley (Halstead and others, 2010). Canals associated with rice agriculture can provide marsh-like habitat conditions throughout the active season of giant gartersnakes (late March–early October; Wylie and others, 2009), and rice fields are emergent wetlands for a part of the active season.

Giant gartersnakes feed primarily on small fish, frogs, and tadpoles (Rossman and others, 1996). Specific prey include tadpoles and small adults of American bullfrogs (*Lithobates catesbeianus*) and tadpoles and adults of sierran treefrogs (*Pseudacris sierra*). Fish prey include but are not limited to mosquitofish (*Gambusia affinis)* and small cyprinid (Cyprinidae spp.) and centrarchid (Centrarchidae spp.) fishes. Little is known about the diet of juvenile giant gartersnakes.

Giant gartersnakes are the longest species of gartersnake (Rossman and others, 1996). Like most natricine (Natricinae spp.) snakes, giant gartersnakes are sexually dimorphic in size, with females the larger sex (Wylie and others, 2010). Like most reptiles, small giant gartersnakes grow faster than large giant gartersnakes (Coates and others, 2009). Males and females exhibit differing seasonal growth patterns, with males forgoing foraging (and growth) for reproductive opportunities in the early spring (Coates and others, 2009). Similarly, male body condition is much lower than female body condition during the spring mating season, but males and females enter brumation in similar condition (Coates and others, 2009). Body condition might be related to the thermal ecology of giant gartersnakes. Female giant gartersnakes exhibit elevated body temperatures during June, July, and August (Wylie and others, 2009), which is the period when they are gravid. In contrast, males exhibit elevated body temperatures in the winter and early spring (Wylie and others, 2009), likely to prepare for the spring mating season. Elevated body temperature of males might be metabolically costly, causing decreased body condition for male snakes in spring.

Although some aspects of the demography of giant gartersnakes are difficult to determine, detailed study of populations in the Sacramento Valley has yielded some insight into their population ecology. Giant gartersnakes in the Sacramento Valley tend to produce smaller litters than those historically observed in the San Joaquin Valley. In the San Joaquin Valley, mean litter size was 23 (standard deviation=9.06; Hansen and Hansen, 1990). In the Sacramento Valley, mean litter size was 17 (95-percent confidence interval [CI]=13–21; Halstead and others, 2011a). Mean parturition date was August 13, although parturition can occur from early July through early October (Halstead and others, 2011a). Neonates in the Sacramento Valley are born with a snout-vent length (SVL) of about 209 mm, and a mass of about 4.9 g (Halstead and others, 2011a). Litter size varies interannually, is potentially linked to resource availability, and large females produce more, rather than larger, offspring (Halstead and others, 2011a).

Survival of adult female giant gartersnakes in the Sacramento Valley varies among sites and years. At an average site in an average year, annual survival probability of adult females greater than 180 g was 0.61 (95-percent CI=0.41–0.79; Halstead and others, 2012). Individuals are at 2.6 times (1.1–11.1) greater daily risk of mortality in aquatic habitats than in terrestrial habitats (Halstead and others, 2012), likely because most terrestrial locations occur when snakes are in refuges, such as under vegetation or in burrows. The effect of linear habitats (that is, canals or streams) on daily risk of mortality varied with context; in rice-growing agricultural systems, daily risk of mortality was less in canals than away from canals, but in systems with natural or restored marshes, risk of mortality was less in these two-dimensional habitats than in simple linear canals (Halstead and others, 2012). Overall survival was greatest in a site with a relatively large network of restored marshes (Halstead and others, 2012).

Abundance, density, and body condition of giant gartersnakes vary by site, presumably as a result of differences in habitat between sites. Abundances and densities were greatest in a natural wetland, less in a natural wetland modified for agricultural uses, less still in rice agriculture, and least in seasonal marshes managed for waterfowl (moist soil management in summer, flooded in winter; Wylie and others, 2010). Body condition of females followed a similar pattern (Wylie and others, 2010). Habitats that resemble natural marshes, therefore, are most likely to support dense populations of healthy giant gartersnakes.

Prior to settlement, the range of giant gartersnakes extended from Butte County in the north to Kern County in the south (Fitch, 1940; Hansen and Brode, 1980). The draining of wetlands and subsequent urban and agricultural development contributed to the loss of more than 90 percent of wetlands in the Central Valley (Frayer and others, 1989). The few remaining natural wetlands are fragmented and the natural cycle of seasonal valley flooding by High Sierra snowmelt has been limited as water presently is diverted by a network of dams and levees. As a result, giant gartersnake populations have become fragmented, with only small isolated populations remaining in the San Joaquin Valley. These factors precipitated the listing of giant gartersnakes by the State of California (California Department of Fish and Game Commission, 1971), and later by the U.S. Fish and Wildlife Service, as a threatened species with a recovery priority designation of 2C: full species, high degree of threat, and high recovery potential (U.S. Fish and Wildlife Service, 1993, 1999).

Giant Gartersnake Occupancy Rates in Sacramento Valley

The purposes of determining giant gartersnake occupancy rates in the Sacramento Valley were (1) to estimate what proportion of Sacramento Valley wetlands (broadly defined to include rice agriculture and its supporting water conveyance structures) is occupied by giant gartersnakes and what variables (landscape-scale habitat, local microhabitat, vegetation composition, and prey counts) correlate with the probability that a site is occupied, and (2) to provide an estimate of occurrence probability to which future estimates can be compared. Evaluation of trends in the probability of occurrence cannot be meaningfully estimated for 2011, 2012, and 2013 because different sites were monitored each year, but this research will serve as a baseline for future monitoring efforts. Occupancy does not necessarily correlate with abundance, survival, or other demographic rates; rather, it is a metric to evaluate the distribution of giant gartersnakes and, over time, to evaluate their colonization and extirpation dynamics.

Methods

Field Methods

We monitored occurrence of giant gartersnakes in randomly selected 25-km^2 grid cells in the Sacramento Valley in 2011 and 2012. We selected the size of grid cells to provide a large number of potential sampling units within our sampling frame, and to include sampling units that were large enough to increase the likelihood of at least one landowner granting permission to sample on his or her property. Grid cells only were considered for selection if they contained at least some rice agriculture and occurred in recovery units outlined in the Draft Recovery Plan for the Giant Gartersnake (U.S. Fish and Wildlife Service, 1999). We used the presence of rice agriculture rather than the presence of wetlands because the intended inference of the project was rice-growing regions of the Sacramento Valley, and the presence of wetlands did not limit the region of inference (all grid cells had at least some wetland habitat within them). The realization of site selection was not random in a strict sense, however, because of failure to obtain permission to sample on private lands within many grid cells. Because of this, and to increase sample sizes, we also incorporated sites at which we were granted access through another program (four sites sampled in 2011 were participants in the California Waterfowl Association's duck brood habitat program), and in 2013 we engaged willing landowners rather than randomly selecting sites, with attempts made to select sites in areas distant from those sampled in previous years (fig. 1).

We did not sample sites at which the occurrence status of giant gartersnakes was known *a priori*. Sites consisted of canals adjacent to rice and wetlands, and selection of sampled units was stratified by basin (American Basin, Butte Basin, Colusa Basin, Sutter Basin, and Yolo Basin) to ensure broad geographic representation. In each site, we deployed trap transects composed of floating galvanized minnow traps (Casazza and others, 2000; Halstead and others, 2013) for a target duration of 21 days each between (1) May 18 and September 28, 2011; (2) June 8 and September 14, 2012; and (3) June 14 and September 13, 2013. In 2012, traps were modified to contain one-way valves constructed from cable ties placed in the small opening of the funnels. In 2013, traps were further modified to include two pieces of hardware cloth attached to each end of the funnel using cable ties (Halstead and others, 2013). These modifications help to direct snakes moving along the edge of a habitat into the trap and to retain the snake within it.

Figure 1. Area of inference, locations sampled for giant gartersnakes (*Thamnophis gigas*), historical habitats, and habitat suitability for giant gartersnakes in the Sacramento Valley, California, 2011–2013.

At selected sites, we placed transects based on landowner permission and field observations of habitat so as to maximize the likelihood of detecting giant gartersnakes. Where possible, we deployed two transects of 50 traps at each monitored site, with traps spaced about 10 m apart. Because of limited appropriate habitat at some sites, we only deployed one transect or deployed fewer than 50 traps per transect at some sites. We positioned transects along the banks of canals or at the edge of emergent vegetation in wetlands because giant gartersnakes forage along habitat edges and habitat edges also act as natural drift fences that direct snake movement to traps.

We primarily used a removal design, whereby the traps remained deployed and were checked daily until we captured a giant gartersnake or we reached the target 21-day deployment duration, whichever came first. We selected 21 days as the maximum duration of sampling at a site based on the findings of previous research and the trade-offs involved in monitoring fewer sites more intensively or more sites less intensively (MacKenzie and Royle, 2005; Bailey and others, 2007; Halstead and others, 2011b). Because we used modified traps in 2012 and 2013 and we obtained permission to sample fewer sites than expected, we did not use a strict removal design. Use of a strict removal design also was occasionally precluded in all years by the lack of a new site to which traps could be moved upon the capture of a giant gartersnake. These deviations from a strict removal design do not affect our inference about occurrence, but do improve the precision of estimates of detection probability relative to a strict removal design. Our sampling effort totaled 23,033 trap-days at 16 sites in 2011, 15,629 trap-days at 8 sites in 2012, and 17,400 trap-days at 11 sites in 2013.

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

We also characterized habitat and vegetation associated with the sampled locations at each site. We recorded the Universal Transverse Mercator coordinates of all trap locations and conducted vegetation and habitat surveys at points along and adjacent to each transect. We visually estimated the percent cover of habitat types (water, submerged vegetation, floating vegetation, emergent vegetation, terrestrial vegetation, rock, or bare ground) and vegetative composition (species or lowest discernible taxonomic category, in some cases divided by growth habit) within a 0.5-m radius of each trap. For each trap location, we randomly selected a point to the left (odd-numbered traps) or right (even-numbered traps) of the transect (as viewed in ascending trap number) at a randomly selected perpendicular distance of 2–5 m where we then visually estimated percent cover of habitats and vegetative composition within a 1-m diameter circle to better characterize habitat surrounding the traps.

We measured, sexed, and uniquely marked each captured giant gartersnake. We used scale measurements (Rossman and others, 1996) to verify the species of each captured gartersnake. We measured snout-vent length and tail length of each individual to the nearest 1.0 mm, and weighed each individual to the nearest 1.0 g. We determined the sex of the individuals by probing the cloaca to detect the presence or absence of hemipenes. After examination, each individual was given a unique brand on its ventral scales (Winne and others, 2006) and, if large enough (>50 g), the individual was implanted with a passive integrated transponder (PIT) tag. Each individual was released at its location of capture immediately after processing.

Analytical Methods

We used single-season occupancy models (MacKenzie and others, 2002, 2006; Kéry 2010; Kéry and Schaub, 2011) to examine patterns in the probability of occurrence (ψ) of giant gartersnakes in the Sacramento Valley. We treated the collection of trap transects associated with a selected grid cell as a site for analysis. We evaluated five different model sets for covariates with ψ:

1. Contemporary and historical variables available in a geographic information system (GIS) that could be used to predict patterns of giant gartersnake occurrence across the landscape,
2. Site-specific microhabitat characteristics,
3. Site-specific vegetation composition,
4. Relative prey counts, and
5. A composite model consisting of GIS, site-specific habitat, and relative prey count variables and interaction terms found important (posterior probability greater than the null model) in model sets 1–4.

The GIS variables we examined included proportion rice, proportion wetland, canal density, and distance to historical tule marsh. We selected the proportion and density habitat variables based on a previous habitat suitability analysis (Halstead and others, 2010), and calculated proportions and densities within a 2.5-km buffer of each transect. Proportional habitat variables were digitized based on imagery from the U.S. Department of Agriculture 2010 National Agricultural Imagery Program, and canal density was based on data from the U.S. Geological Survey (2015). We selected historical tule marsh habitat because it represented likely locations of historically suitable habitat. Rice agriculture is widespread in the parts of the Sacramento Valley we sampled, and we hypothesized that distance to historical habitat might explain current distribution patterns for the giant gartersnake. We calculated the distance from each trap to historical tule marsh (based on Küchler, 1977) using the Near tool in ArcGIS™ 10.2.2 (Environmental Systems Research Institute, 2014). To obtain a site-specific covariate for distance to historical tule marsh, we calculated the mean distance to historical tule marsh within each sample site. We also tested the interaction between distance to historical marsh and proportion rice, proportion wetland, and canal density because historical marsh was determined to be important in a previous analysis of a subset of these data (Halstead and others, 2014), and the larger sample of sites considered here allowed the fitting of models with more parameters. These interactions might better explain patterns in the probability of occurrence of giant gartersnakes because they essentially correct the probability of occurrence, based on contemporary habitat, for the distance to historical habitat.

The four local microhabitat variables we selected also were based on the ecology of giant gartersnakes. We used proportion emergent vegetation because we hypothesized that it would provide cover and foraging locations for giant gartersnakes, thereby increasing ψ. Similar logic was used for proportion submerged vegetation, which we expected to provide rich prey communities. Although we hypothesize that a nonlinear relation exists with emergent and submerged vegetation (for example, a quadratic relation such that the relation of percent cover with ψ is positive at low cover values, but negative at high cover values), the maximum observed cover for these microhabitats was 56.8 and 12.8 percent, respectively. We, therefore, did not attempt to fit quadratic effects of these habitat types on ψ.

We further hypothesized that proportion floating vegetation, which often forms thick mats during the active season of giant gartersnakes (April–September; Wylie and others, 2009), would negatively affect ψ because of its potential negative effects on prey communities, inhibition of locomotion by giant gartersnakes, or other mechanisms. We also hypothesized that terrestrial vegetation would have a positive effect on ψ because it would provide cover for giant gartersnakes moving to and from terrestrial refuges, and would also act as an indicator of the level of disturbance to a site. Microhabitat variables that we collected in the field but did not use in analysis included open water, litter, bare ground, and rock. We did not use these additional microhabitat variables because open water was correlated with floating vegetation, and other variables were rare or expected to have weaker relations with giant gartersnake occurrence. Just as with the GIS variable selection, we included interactions of local microhabitat variables with distance to historical tule marsh habitat in this model set.

We focused on common aquatic vegetation types for the analysis of the effects of vegetation on the occurrence of giant gartersnakes. We expected proportion tule (*Schoenoplectus acutus*), the dominant historical marsh vegetation in the Sacramento Valley (Garone, 2007), to be positively related to ψ. Proportion cattail (*Typha* spp.) and proportion water primrose (*Ludwigia* spp.) similarly were expected to increase ψ because of the cover and structure they can provide for giant gartersnakes at the proportions observed at sampled locations (maximum proportion cattail = 0.21; maximum proportion water primrose = 0.58). We expected that proportion mosquitofern (*Azolla* spp.), which can form dense floating mats, would be negatively related to ψ for the same reasons as floating vegetation in general. Vegetation variables collected in the field but not used in analysis included proportion duckweed (Lemnoideae spp.), proportion algae, proportion coontail (*Ceratophyllum demersum*), proportion watermilfoil (*Myriophyllum* spp.), proportion sedges (Cyperaceae spp.), proportion rushes (Juncaceae spp.), proportion knotweed (*Polygonum* spp.), proportion arrowhead (*Sagittaria* spp.), proportion watergrass (*Echinochloa* spp.), proportion rice (*Oryza* spp.), proportion turf grasses (Poacea spp.), proportion bunch grasses (Poaceae spp.), proportion herbaceous dicots, proportion shrubs, proportion blackberry (*Rubus* spp.), and proportion grape (*Vitis* spp.). These other vegetation variables were not included because they were rare or did not have a hypothesized relation with giant gartersnake occurrence. We also included interactions of vegetation with distance to historical tule marsh habitat in the vegetation model set.

We examined three major categories of prey as predictors of giant gartersnake occurrence, as well as their interaction with distance to historical marsh as we did with all other model sets. We examined adult and larval anurans separately because of their different body plans and primary habitats. Anurans at our study sites consisted primarily of introduced American bullfrogs. We grouped all fishes together for analysis. Fish communities at our sites were predominantly introduced species, including mosquitofish, several species of Centrarchidae, common carp (*Cyprinus carpio*) and other introduced Cyprinidae, and bullhead catfish (*Ameiurus* spp.). We hypothesized that all prey species would be positively related to ψ. We calculated the mean number of prey of each category per trap at each site for further analysis.

We analyzed all models (coupled logistic regression models for predictors of occurrence and detection) using Bayesian methods. The logistic regression models are coupled because the opportunity for giant gartersnakes to be detected at a site is conditional upon their occurrence at the site. We defined sample units as the collection of trap-transects deployed within a grid cell. We used the same observation model for detection probability (p) with each model set. We used variables identified in Halstead and others (2011b) as predictors for p, and used informative priors based on data collected in similar traps and habitats in the Sacramento Valley from 2003 to 2009 (table 1). We controlled for a different number of traps at different sites and for variations in the daily number of active traps within sites by using daily trap number as a predictor variable for detection probability. Use of a removal design, whereby different sites are sampled a different number of times depending on whether the species was detected, does not affect inference about occupancy, but it does limit flexibility in modelling the detection process (Mackenzie and Royle, 2005). The use of informative priors should improve the efficiency of the removal design, which provides less information about the detection process than a balanced study design (Mackenzie and Royle, 2005). Because we used modified traps in 2012 and 2013, we included a variable for the use of each type of modified trap in the detection model. Because we only used a single trap type in each year, the effects of trap type and year on p cannot be separated. Unlike with the other detection variables, we gave modified traps a vague prior distribution (table 1). To evaluate the sensitivity of our results to the use of informative priors, we also ran each model using vague priors on all detection parameters (table 1).

We analyzed each occurrence model set separately. We quantified the probability of all subsets of the full additive model plus interactions with distance to historical tule marsh for each model set using indicator variables on model coefficients (Kuo and Mallick, 1998; Royle and Dorazio, 2008). Briefly, each model coefficient was multiplied by an independent indicator variable with a vague *Bern(0.5)* prior, which gave equal prior probability to all models in the model set (0.0625 in an additive models-only model set containing four variables; models including interactions are given reduced prior probabilities relative to main effects because both main effects and the interaction must occur in the model). If the interaction of any variable with historical marsh was not supported, we re-fit the model using only additive effects because main effects in the presence of an interaction have different meaning and value than in the absence of an interaction. For model sets in which an interaction was supported, model-averaging was done separately for iterations in which the interaction was and was not supported. We used vague *N(0,1.65)* (mean, standard deviation) priors, which are approximately uniform on the probability scale (Lunn and others, 2013), for all model coefficients (which are on the logit scale). We standardized all predictor variables to mean zero and unit variance prior to analysis. Posterior inference was based on five chains of 6,000 iterations each, after a burn-in period of 2,000 iterations. We thinned each chain by a factor of 2, keeping 10,000 iterations to describe the posterior distribution of each parameter. We analyzed each model with JAGS software, version 3.4.0 (Plummer, 2015a) called from R language version 3.2.1 (R Core Team, 2015) using the rjags software package (Plummer, 2015b). We diagnosed convergence with visual examination of history plots and with the Gelman-Rubin statistic (Gelman and Rubin, 1992); no evidence for lack of convergence was observed.

Table 1. Prior probability distributions for model parameters used in analysis.

[Informative priors are based on data collected in Sacramento Valley, California, 2003–2009. Normal distributions are given as *N(mean, standard deviation)*. GIS, geographic information system; veg., vegetation].

Model component	Model set	Parameter	Symbol	Prior probability	
				Informative	Vague
Detection	All	Intercept	α_0	*N(-2.02,0.133)*	*N(0,1.65)*
		Effect of water temperature	α_{tw}	*N(0.277,0.052)*	*N(0,1.65)*
		Effect of date	α_{date}	*N(-0.307,0.059)*	*N(0,1.65)*
		Effect of number of traps	α_{ntrap}	*N(0.321,0.118)*	*N(0,1.65)*
		Effect of trap modification	α_{tm}	*N(0,1.65)*	*N(0,1.65)*
		Random site effect	ε_{site}	*Gamma(100.4,98.5)*	*Uniform(0,10)*
Occurrence	All	Intercept	β_0	*N(0,1.65)*	*N(0,1.65)*
	GIS	Effect of proportion rice	β_{rice}	*N(0,1.65)*	*N(0,1.65)*
		Effect of proportion wetland	β_{wet}	*N(0,1.65)*	*N(0,1.65)*
		Effect of canal density	β_{canal}	*N(0,1.65)*	*N(0,1.65)*
		Effect of distance to historical marsh	β_{hm}	*N(0,1.65)*	*N(0,1.65)*
		Effect of interaction between historical marsh and proportion rice	$\beta_{hmXrice}$	*N(0,1.65)*	*N(0,1.65)*
		Effect of interaction between historical marsh and proportion wetland	β_{hmXwet}	*N(0,1.65)*	*N(0,1.65)*
		Effect of interaction between historical marsh and canal density	$\beta_{hmXcanal}$	*N(0,1.65)*	*N(0,1.65)*
	Local habitat	Effect of proportion emergent veg.	β_{ev}	*N(0,1.65)*	*N(0,1.65)*
		Effect of proportion submerged veg.	β_{sv}	*N(0,1.65)*	*N(0,1.65)*
		Effect of proportion floating veg.	β_{fv}	*N(0,1.65)*	*N(0,1.65)*
		Effect of proportion terrestrial veg.	β_{tv}	*N(0,1.65)*	*N(0,1.65)*
		Effect of distance to historical marsh	β_{hm}	*N(0,1.65)*	*N(0,1.65)*
		Effect of interaction between historical marsh and proportion emerged veg.	β_{hmXev}	*N(0,1.65)*	*N(0,1.65)*
		Effect of interaction between historical marsh and proportion submerged veg.	β_{hmXsv}	*N(0,1.65)*	*N(0,1.65)*
		Effect of interaction between historical marsh and proportion floating veg.	β_{hmXfv}	*N(0,1.65)*	*N(0,1.65)*
		Effect of interaction between historical marsh and proportion terrestrial veg.	β_{hmXtv}	*N(0,1.65)*	*N(0,1.65)*

Model component	Model set	Parameter	Symbol	Prior probability	
				Informative	Vague
	Local vegetation	Effect of proportion tule	β_{tule}	$N(0,1.65)$	$N(0,1.65)$
		Effect of proportion cattail	β_{ct}	$N(0,1.65)$	$N(0,1.65)$
		Effect of proportion water primrose	β_{wp}	$N(0,1.65)$	$N(0,1.65)$
		Effect of proportion mosquitofern	β_{mf}	$N(0,1.65)$	$N(0,1.65)$
		Effect of distance to historical marsh	β_{hm}	$N(0,1.65)$	$N(0,1.65)$
		Effect of interaction between historical marsh and proportion tule	$\beta_{hmXtule}$	$N(0,1.65)$	$N(0,1.65)$
		Effect of interaction between historical marsh and proportion cattail	β_{hmXct}	$N(0,1.65)$	$N(0,1.65)$
		Effect of interaction between historical marsh and proportion water primrose	β_{hmXwp}	$N(0,1.65)$	$N(0,1.65)$
		Effect of interaction between historical marsh and proportion mosquitofern	β_{hmXmf}	$N(0,1.65)$	$N(0,1.65)$
	Prey	Effect of tadpole count	β_{tad}	$N(0,1.65)$	$N(0,1.65)$
		Effect of frog count	β_{frog}	$N(0,1.65)$	$N(0,1.65)$
		Effect of fish count	β_{fish}	$N(0,1.65)$	$N(0,1.65)$
		Effect of distance to historical marsh	β_{hm}	$N(0,1.65)$	$N(0,1.65)$
		Effect of interaction between historical marsh and tadpole count	β_{hmXtad}	$N(0,1.65)$	$N(0,1.65)$
		Effect of interaction between historical marsh and frog count	$\beta_{hmXfrog}$	$N(0,1.65)$	$N(0,1.65)$
		Effect of interaction between historical marsh and fish count	$\beta_{hmXfish}$	$N(0,1.65)$	$N(0,1.65)$
	Composite	Effect of distance to historical marsh	β_{hm}	$N(0,1.65)$	$N(0,1.65)$
		Effect of proportion submerged veg.	β_{sv}	$N(0,1.65)$	$N(0,1.65)$
		Effect of fish count	β_{fish}	$N(0,1.65)$	$N(0,1.65)$
		Effect of interaction between historical marsh and proportion submerged veg.	β_{hmXsv}	$N(0,1.65)$	$N(0,1.65)$

Results

We detected giant gartersnakes at 16 of 35 sampled sites. For the GIS-level analysis, models containing an effect of distance to historical marsh had the greatest support from the data, but considerable model selection uncertainty existed (table 2). The posterior probability of the model with an effect of historical tule marsh (and no other effects) on ψ was 0.171 with informative priors (0.102 with vague priors); the null model had a posterior probability of 0.141 with informative priors (0.061 with vague priors; table 2). The probability that historical marsh affected ψ across all models was 0.526. Model-averaged β_{hm} based on the full additive model (including all submodels) and using informative priors was -0.03 (95-percent credible interval=-1.54–0.03). Inference about β_{hm} was similar, but slightly less precise, with the use of informative priors on detection parameters (β_{hm} with vague priors = -0.12 [-2.43–0.31]).

For the model set based on local microhabitat conditions, the model with an effect of submerged vegetation, distance to historical marsh, and their interaction had the greatest posterior probability (0.165 with informative priors; 0.113 with vague priors), although considerable model selection uncertainty existed (table 3). Model-averaged β_{sv}, β_{hm}, and β_{hmXsv} using informative priors were 0.00 (-1.97–1.11), -0.28 (-1.75–0.43), and 0.00 (95-percent CI=0.00–3.74), respectively. Vague priors resulted in similar, but less precise, posterior inference about these parameters (β_{sv}=0.00 [-2.71–1.78], β_{hm}=-0.46 [-2.54–0.45], and β_{hmXsv}=0.00 [-0.01–4.00]).

For the model set based on local vegetation composition, the model with an effect of distance to historical marsh on ψ had the greatest posterior probability (0.186); the null model was ranked second with a posterior probability of 0.133 (table 4). As for GIS-level and local microhabitat analyses, considerable model selection uncertainty existed among the models comprising the vegetation composition model set. Using vague priors, effect of distance to historical marsh also had the greatest posterior probability (0.102), followed by the null model (0.085). Model-averaged β_{hm} was -0.17 (-1.66–0.00) with informative priors, and -0.36 (-2.45–0.10) with vague priors.

For the model set based on mean prey counts, the model with an effect of relative fish count and distance to historical marsh had the greatest posterior probability (0.160), and the model with an effect of relative fish count only was ranked second (0.151) using informative priors. The two models with the greatest posterior probability using vague priors were the same two models as those with the greatest posterior probability using informative priors, although their ranking was reversed (posterior probabilities=0.095 and 0.118, respectively; table 5). Model-averaged effect of relative fish count on ψ was -0.75 (-2.34–0.00) with informative priors and -1.11 (-3.71–0.02) with vague priors. Model-averaged effect of distance to historical marsh on ψ was -0.56 (-1.93–0.00) with informative priors and -0.42 (-2.45–0.07) with vague priors.

Table 2. Model selection results for occupancy of giant gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 2011–2013, based on geographic information system-derived landscape habitat variables.

[A "1" indicates that the variable was included in the model; a "0" indicates that it was omitted from the model. Models are listed in order of decreasing support under informative priors. Only models with a posterior probability greater than 0.01 under either set of priors are shown. Parameters are defined in table 1]

Parameter							Posterior probability	
β_{rice}	β_{wet}	β_{hm}	β_{canal}	$\beta_{hmXrice}$	β_{hmXwet}	$\beta_{hmXcanal}$	Informative	Vague
0	0	1	0	0	0	0	0.171	0.102
0	0	0	0	0	0	0	0.141	0.061
1	0	0	0	0	0	0	0.111	0.087
0	0	1	1	0	0	1	0.074	0.078
0	0	0	1	0	0	0	0.069	0.073
1	0	1	0	0	0	0	0.063	0.059
1	1	0	0	0	0	0	0.045	0.045
0	0	1	1	0	0	0	0.043	0.076
1	0	0	1	0	0	0	0.042	0.070
0	1	0	0	0	0	0	0.031	0.023
0	1	1	0	0	0	0	0.029	0.018
1	0	1	0	1	0	0	0.020	0.028
0	1	1	1	0	0	1	0.018	0.020
1	1	0	1	0	0	0	0.017	0.034
0	1	0	1	0	0	0	0.017	0.028
0	1	1	0	0	1	0	0.015	0.009
1	0	1	1	0	0	1	0.012	0.023
1	0	1	1	0	0	0	0.011	0.021
1	1	1	0	0	0	0	0.009	0.013
0	1	1	1	0	0	0	0.005	0.023
1	0	1	1	1	0	1	0.007	0.021
1	0	1	1	1	0	0	0.007	0.013
0	1	1	1	0	1	0	0.002	0.011

Table 3. Model selection results for occupancy of giant gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 2011–2013, based on local microhabitats.

[A "1" indicates that the variable was included in the model; a "0" indicates that it was omitted from the model. Models are listed in order of decreasing support under informative priors. Only models with a posterior probability greater than 0.01 under either set of priors are shown. Parameters are defined in table 1]

Parameter									Posterior probability	
β_{ev}	β_{sv}	β_{tv}	β_{fv}	β_{hm}	β_{hmXev}	β_{hmXsv}	β_{hmXtv}	β_{hmXfv}	Informative	Vague
0	1	0	0	1	0	1	0	0	0.165	0.113
0	0	0	0	1	0	0	0	0	0.105	0.087
0	0	0	0	0	0	0	0	0	0.078	0.042
0	1	0	0	0	0	0	0	0	0.068	0.055
0	1	0	0	1	0	0	0	0	0.055	0.044
1	1	0	0	1	0	1	0	0	0.053	0.035
1	1	0	0	0	0	0	0	0	0.029	0.037
1	0	0	0	0	0	0	0	0	0.025	0.025
0	1	1	0	1	0	1	0	0	0.025	0.029
0	0	0	1	0	0	0	0	0	0.023	0.022
0	1	1	0	0	0	0	0	0	0.022	0.023
0	1	0	1	1	0	1	0	0	0.022	0.023
1	0	0	0	1	0	0	0	0	0.021	0.031
0	0	1	0	0	0	0	0	0	0.021	0.019
1	1	0	0	1	1	1	0	0	0.019	0.023
0	1	0	1	0	0	0	0	0	0.019	0.019
1	1	0	0	1	0	0	0	0	0.017	0.013
0	0	1	0	1	0	0	0	0	0.015	0.014
0	0	0	1	1	0	0	0	0	0.014	0.014
0	1	0	1	1	0	1	0	1	0.013	0.013
1	1	0	1	1	0	1	0	0	0.011	0.009
0	1	1	0	1	0	1	1	0	0.011	0.015
1	1	1	0	0	0	0	0	0	0.005	0.015
1	0	1	0	0	0	0	0	0	0.009	0.014
1	0	0	1	0	0	0	0	0	0.009	0.013
1	1	0	1	0	0	0	0	0	0.009	0.012
1	1	1	0	1	0	1	0	0	0.008	0.011
0	1	0	1	1	0	0	0	0	0.007	0.011
1	0	0	0	1	1	0	0	0	0.007	0.011
0	1	1	0	1	0	0	0	0	0.007	0.011
0	1	1	1	1	0	1	0	0	0.002	0.010

Table 4. Model selection results for occupancy of giant gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 2011–2013, based on local vegetation composition.

[A "1" indicates that the variable was included in the model; a "0" indicates that it was omitted from the model. Models are listed in order of decreasing support under informative priors. Only models with a posterior probability greater than 0.01 under either set of priors are shown. Parameters are defined in table 1]

β_{tule}	β_{ct}	β_{wp}	β_{mf}	β_{hm}	$\beta_{hmXtule}$	β_{hmXct}	β_{hmXwp}	β_{hmXmf}	Informative	Vague
0	0	0	0	1	0	0	0	0	0.186	0.102
0	0	0	0	0	0	0	0	0	0.133	0.085
0	0	1	0	0	0	0	0	0	0.120	0.069
0	0	1	0	1	0	0	0	0	0.047	0.045
0	0	0	1	0	0	0	0	0	0.037	0.039
0	1	0	0	0	0	0	0	0	0.036	0.031
0	0	1	0	1	0	0	1	0	0.036	0.028
1	0	1	0	0	0	0	0	0	0.035	0.025
0	1	1	0	0	0	0	0	0	0.035	0.031
0	0	1	1	0	0	0	0	0	0.035	0.029
1	0	0	0	1	0	0	0	0	0.030	0.029
1	0	0	0	0	0	0	0	0	0.030	0.025
0	0	0	1	1	0	0	0	0	0.030	0.019
0	1	0	0	1	0	0	0	0	0.022	0.033
0	1	0	0	1	0	1	0	0	0.016	0.039
1	0	0	1	0	0	0	0	0	0.015	0.013
1	0	0	0	1	1	0	0	0	0.011	0.019
1	0	1	1	0	0	0	0	0	0.010	0.011
0	1	1	1	0	0	0	0	0	0.010	0.008
0	1	0	1	0	0	0	0	0	0.007	0.018
1	1	0	0	0	0	0	0	0	0.002	0.015
1	1	0	0	1	0	0	0	0	0.003	0.015
1	0	1	0	1	0	0	1	0	0.007	0.011
0	1	1	0	1	0	1	0	0	0.005	0.011
0	1	1	0	1	0	0	1	0	0.003	0.011
0	0	0	1	1	0	0	0	1	0.007	0.011
1	0	0	1	1	1	0	0	0	0.005	0.010
0	1	1	0	1	0	0	0	0	0.005	0.010

Table 5. Model selection results for occupancy of giant gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 2011–2013, based on mean counts of potential prey species in traps.

[A "1" indicates that the variable was included in the model; a "0" indicates that it was omitted from the model. Models are listed in order of decreasing support under informative priors. Only models with a posterior probability greater than 0.01 under either set of priors are shown. Parameters are defined in table 1]

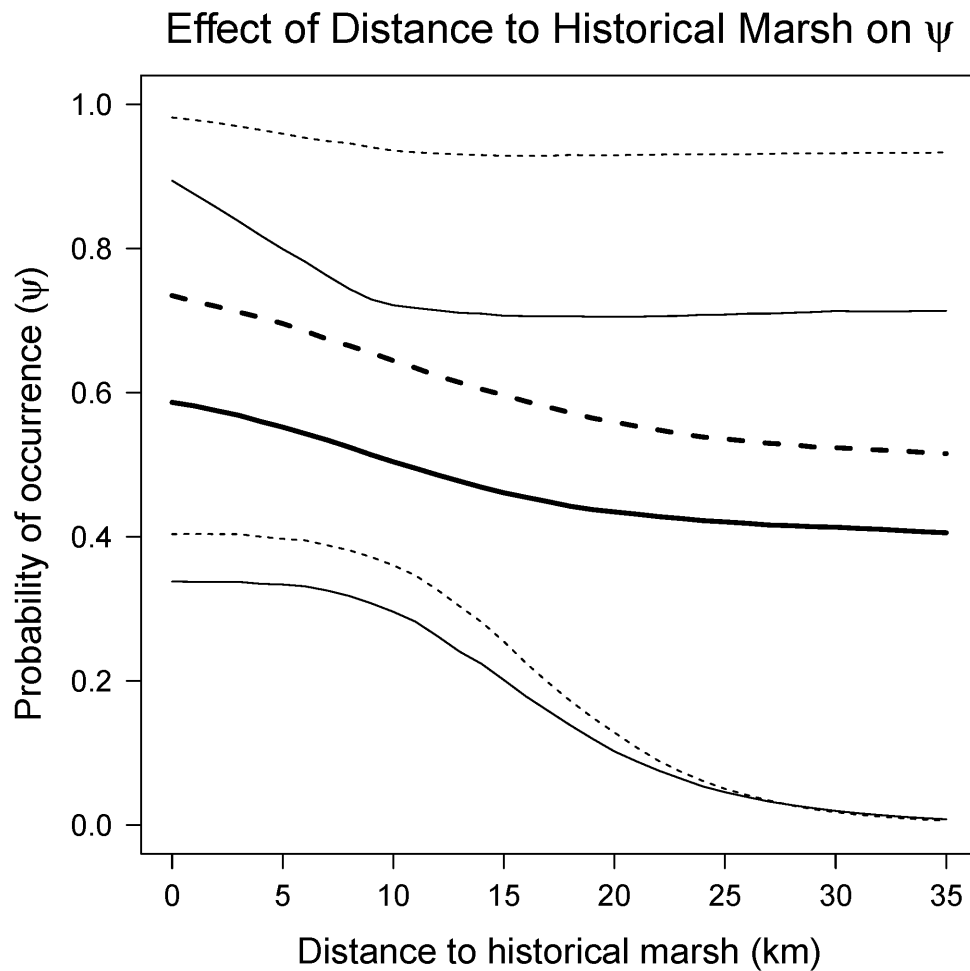| Parameter							Posterior probability	
β_{tad}	β_{frog}	β_{fish}	β_{hm}	β_{hmXtad}	$\beta_{hmXfrog}$	$\beta_{hmXfish}$	Informative	Vague
0	0	1	1	0	0	0	0.160	0.095
0	0	1	0	0	0	0	0.151	0.118
0	0	0	1	0	0	0	0.103	0.067
0	0	1	1	0	0	1	0.085	0.077
0	0	0	0	0	0	0	0.075	0.039
0	1	0	1	0	0	0	0.037	0.039
0	1	1	1	0	1	0	0.031	0.030
1	0	1	1	0	0	0	0.029	0.018
1	0	0	1	0	0	0	0.029	0.033
0	1	1	1	0	0	0	0.026	0.029
0	1	1	0	0	0	0	0.025	0.043
1	0	1	0	0	0	0	0.023	0.033
0	1	1	0	0	1	0	0.023	0.043
0	1	0	0	0	0	0	0.023	0.029
1	0	1	0	1	0	0	0.022	0.028
1	0	1	1	1	0	0	0.019	0.022
0	1	1	1	0	0	1	0.018	0.027
1	0	0	0	0	0	0	0.017	0.017
1	0	1	1	1	0	1	0.015	0.018
0	1	1	1	0	1	1	0.011	0.031
1	0	1	1	0	0	1	0.011	0.019
1	1	0	1	0	0	0	0.010	0.025
1	1	1	0	0	1	0	0.004	0.016
1	1	1	0	1	0	0	0.002	0.015
1	1	1	0	1	1	0	0.002	0.011
1	1	1	0	0	0	0	0.008	0.011
1	1	0	0	0	0	0	0.008	0.011

For the composite analysis, the model with an interaction of distance to historical marsh and submerged vegetation using informative priors had the greatest posterior probability (0.156; table 6). The second-ranked model included additive effects of distance to historical marsh and relative fish count (0.119). Using vague priors, the model with an effect of relative fish count only was ranked first (posterior probability = 0.137), and the second-ranked model included an additive effect of distance to historic marsh and relative fish count (0.115). Model-averaged β_{hm} without interactions indicated a weak negative effect on ψ regardless of priors (β_{hm} with informative priors= 0.00 [-1.75–0.00]; with vague priors=0.00 [-2.25–0.00]; fig. 2). Giant gartersnakes, therefore, were slightly more likely to occur on the floor of the Sacramento Valley near historical drainage basins than at higher elevations along the edge of the Valley (figs. 3 and 4). Distance to historical marsh and proportion submerged vegetation had a positive interaction (model-averaged β_{hmXsv} with informative priors=0.00 [0.00–3.73]; with vague priors=0.00 [0.00–3.46]). Thus, in areas near historical marsh, submerged vegetation had a negative effect on ψ, but this effect became positive as distance from historical marsh increased (fig. 5). Great uncertainty existed in the probability of occurrence at moderate-to-high proportion cover of submerged vegetation at greater distances from historical marsh, primarily because few sampled sites had this combination of variables (fig. 6). Relative fish count had a negative effect on ψ (model-averaged β_{fish} with informative priors=-0.44 [-2.32–0.00]; with vague priors=-0.80 [-3.47–0.07]; fig. 7). Additive effects of submerged vegetation and an interaction of relative fish count with distance to historical marsh were not supported.

Table 6. Model selection results for occupancy of giant gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 2011–2013, based on composite variables from geographic information system-derived landscape, local microhabitat, and relative fish count, including select interactions.
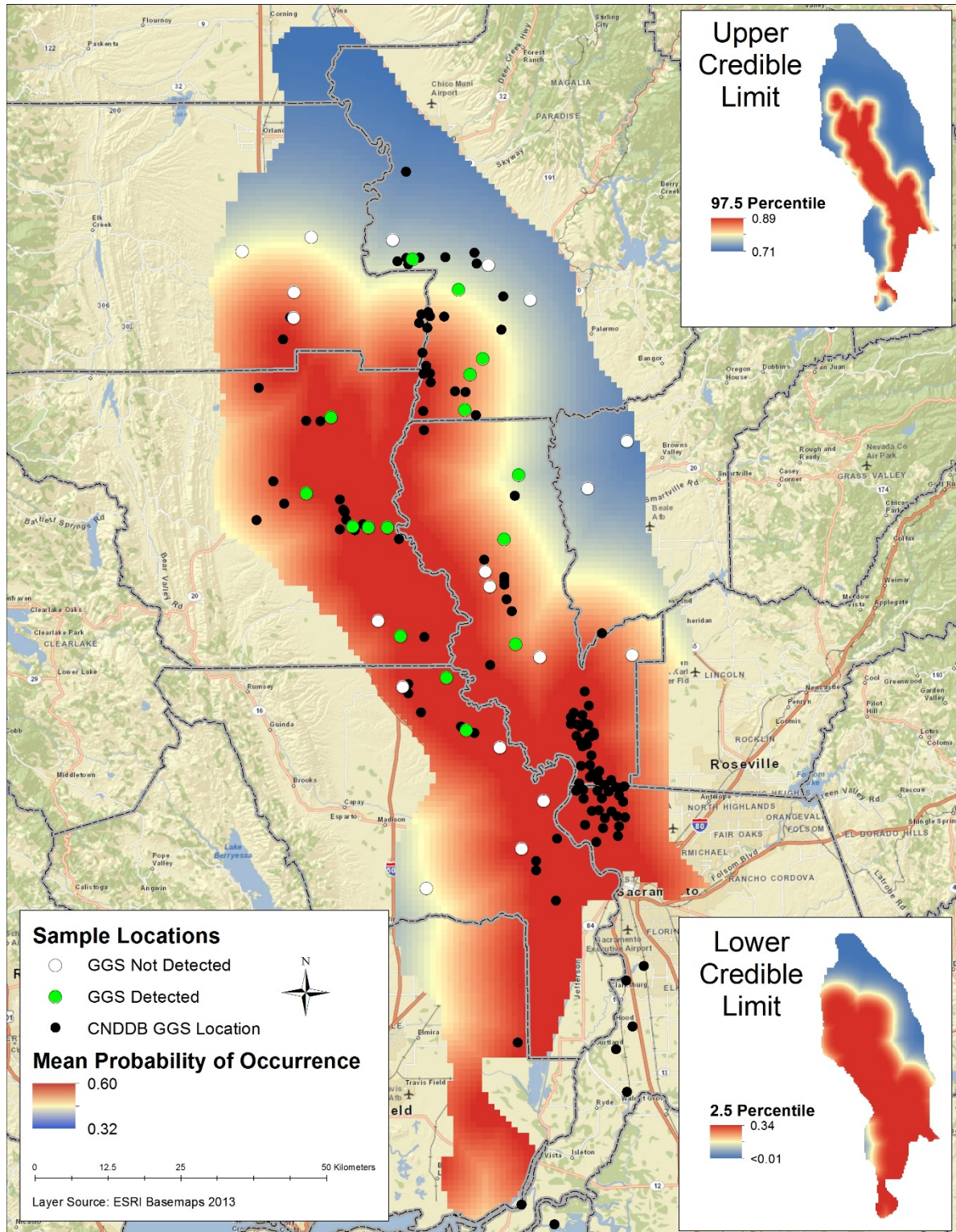
[A "1" indicates that the variable was included in the model; a "0" indicates that it was omitted from the model. Models are listed in order of decreasing support under informative priors. Only models with a greater posterior probability than prior probability (0.077) under either set of priors and the null model are shown. Parameters are defined in table 1]

Parameter					Posterior probability	
β_{hm}	β_{sv}	β_{fish}	β_{hmXsv}	$\beta_{hmXfish}$	Informative	Vague
1	1	0	1	0	0.156	0.100
1	0	1	0	0	0.119	0.115
0	0	1	0	0	0.119	0.137
1	1	1	1	0	0.097	0.086
0	1	1	0	0	0.085	0.115
1	0	0	0	0	0.078	0.066
0	0	0	0	0	0.071	0.048
1	0	1	0	1	0.061	0.089

The effect of using informative priors had much more influence on p than on ψ. Inference using both sets of priors was consistent, with comparable posterior means (fig. 8). The greatest difference between the two sets of priors was that coefficients of the model were estimated with much greater precision using informative priors than with vague priors (fig. 8). Posteriors based on the analysis with informative priors closely matched their prior distributions, and were entirely contained within the posteriors based on vague priors (fig. 8). Under average conditions, posterior mean p using unmodified traps in 2011 was 0.12 (0.09–0.15) based on informative priors, and 0.15 (0.02–0.57) based on vague priors. Based on informative priors, the use of modified traps in 2012 increased the odds of detection to 6.3 times (2.2–18.4) that of unmodified traps, and modified traps used in 2013 increased the odds of detection to 5.6 times (1.5–18.6) that of unmodified traps (fig. 8). The use of vague priors resulted in much greater uncertainty about effect of trap modifications, with odds of detection 3.5 times (0.40–24.7) that of unmodified traps in 2012, and 2.1 times (0.18–19.0) that of unmodified traps in 2013 (fig. 8).
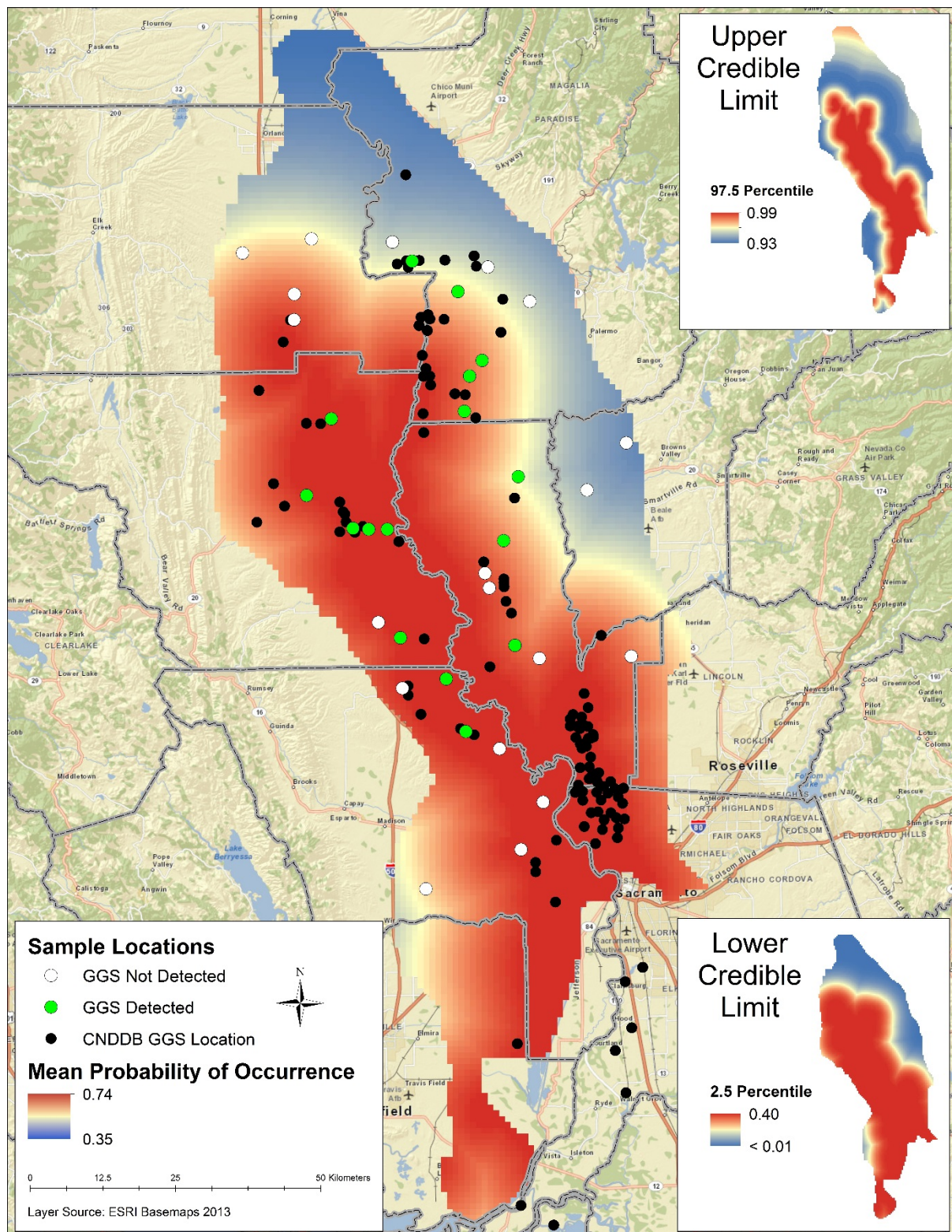

Figure 2. Model-averaged effect of the distance to historical tule marsh on the probability of occurrence of giant gartersnakes (*Thamnophis gigas*) in the rice-growing regions of the Sacramento Valley, California, 2011–2013, based on the composite model set. Only those iterations for which an interaction term of other variables with historical marsh was not included were used in model averaging. Solid lines represent the results of the models using informative priors; dashed lines represent the results of the models using vague priors. Bold lines represent posterior medians; light lines represent the posterior 95-percent credible limits.

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Figure 3. Model-averaged posterior mean probability of occurrence of giant gartersnakes (*Thamnophis gigas*) in the rice-growing regions of the Sacramento Valley, California, 2011–2013, using informative priors.
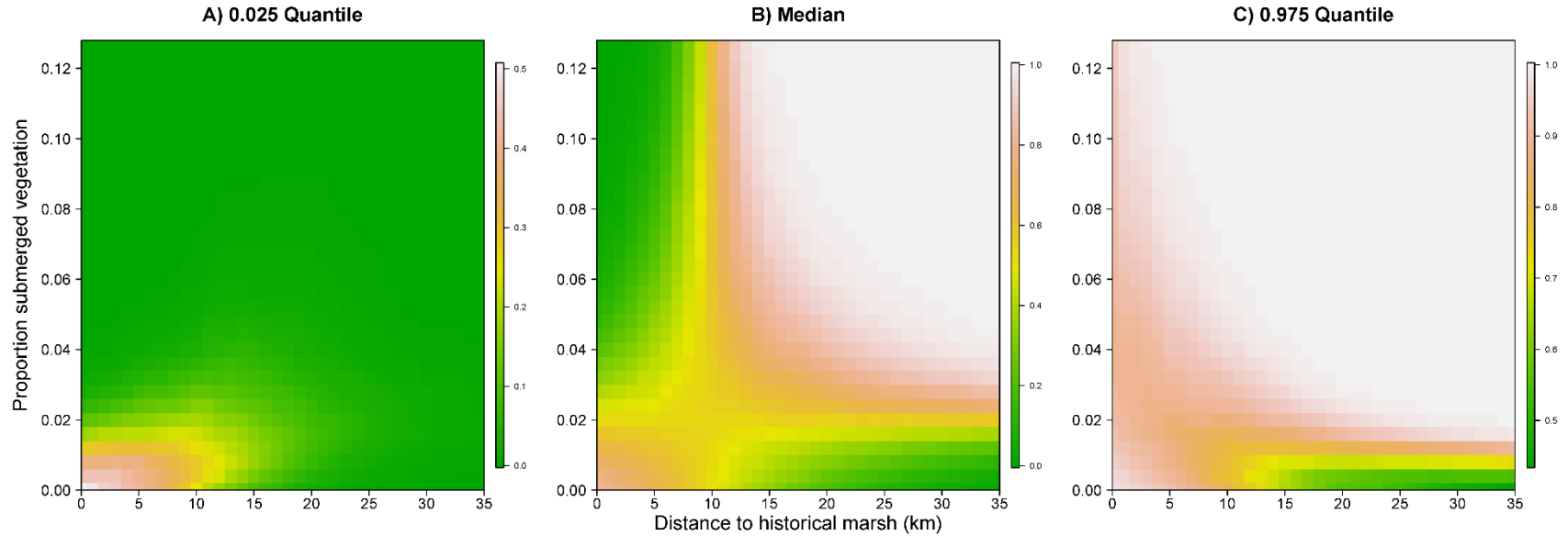
Figure 4. Model-averaged posterior mean probability of occurrence of giant gartersnakes (*Thamnophis gigas*) in the rice-growing regions of the Sacramento Valley, California, 2011–2013, using vague priors.

Figure 5. Effects of the interaction between distance to historical tule marsh and proportion of submerged vegetation on the probability of occurrence of giant gartersnakes (*Thamnophis gigas*) in the rice-growing regions of the Sacramento Valley, California, 2011–2013. (A) 2.5 percentile, (B) median, and (C) 97.5 percentile of the posterior distribution.

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Figure 6. Uncertainty in the probability of occurrence of giant gartersnakes (*Thamnophis gigas*) in the rice-growing regions of the Sacramento Valley, California, 2011–2013, based on the interaction of distance to historical marsh and percent cover of submerged vegetation. Black dots represent sampled locations.
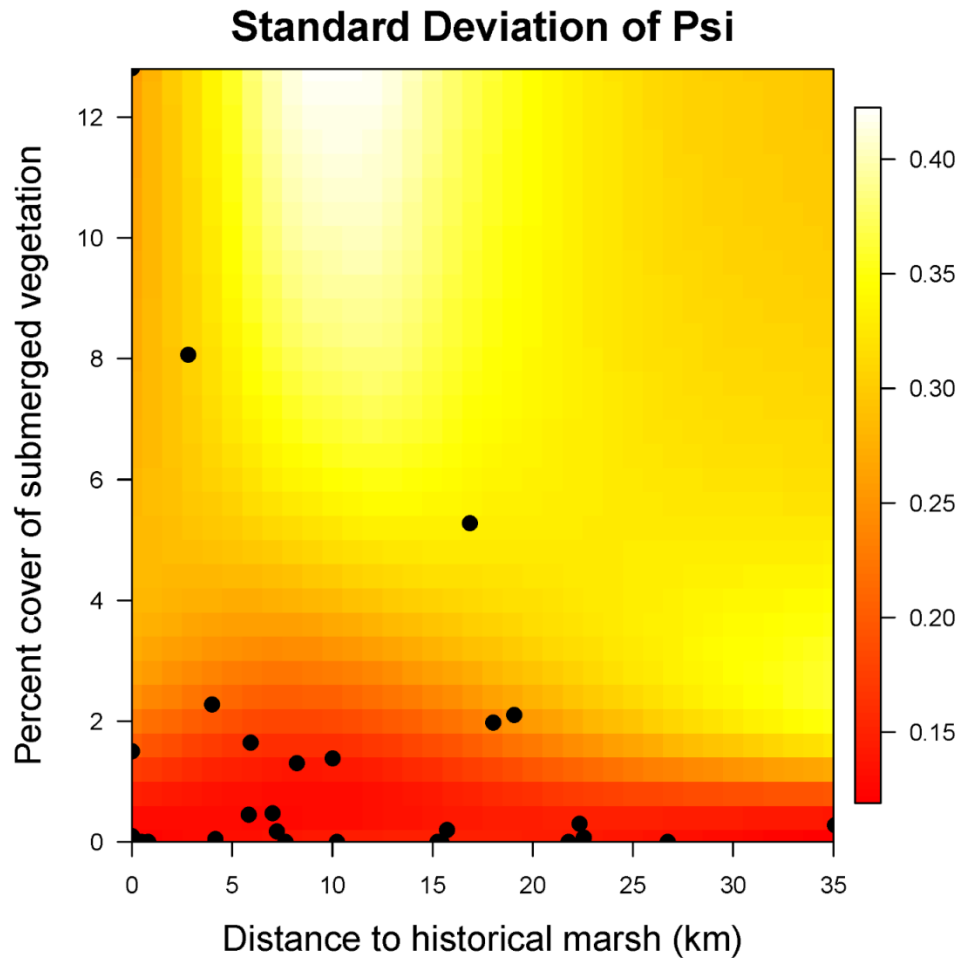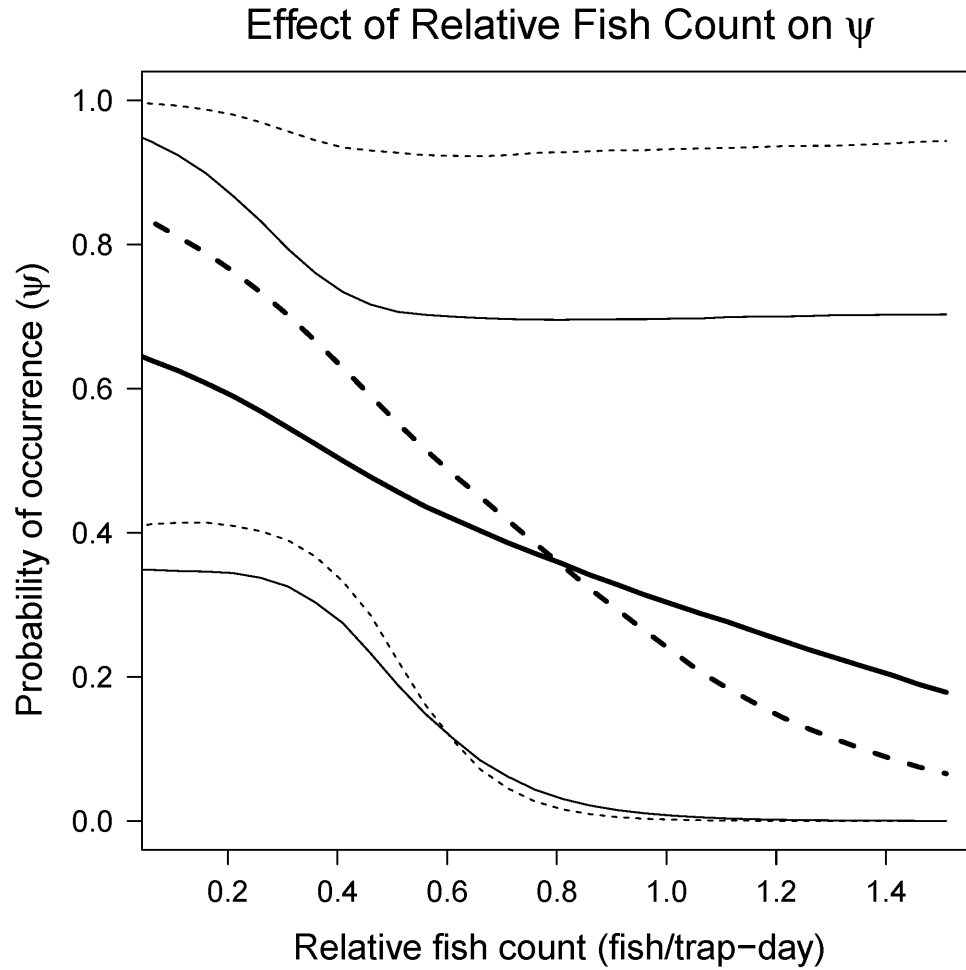
Figure 7. Model-averaged effect of relative fish count on the probability of occurrence of giant gartersnakes (*Thamnophis gigas*) in the rice-growing regions of the Sacramento Valley, California, 2011–2013, based on the compo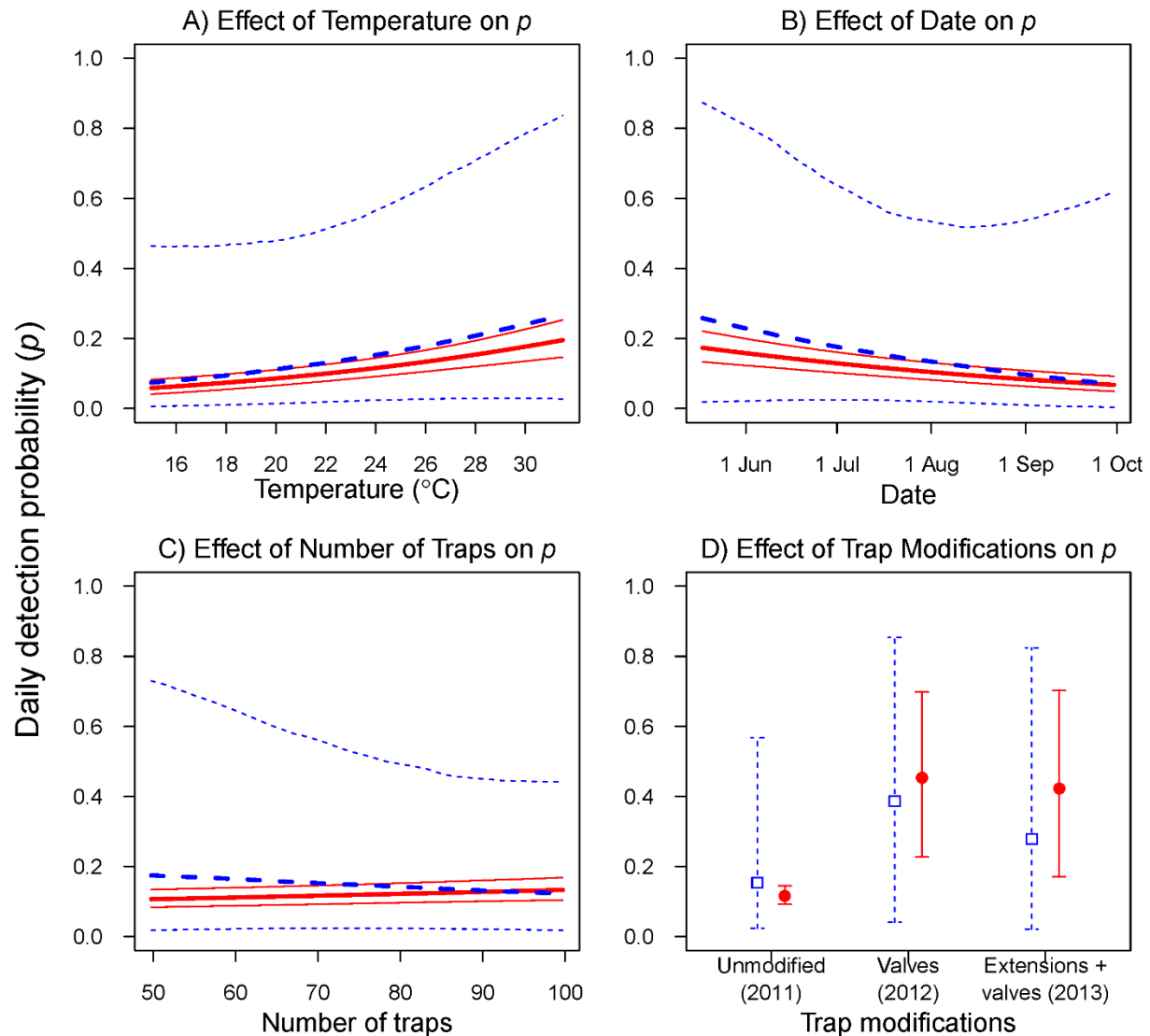site model set. Solid lines represent the results of the models using informative priors; dashed lines represent the results of the models using vague priors. Bold lines represent posterior medians; light lines represent posterior 95-percent credible limits.

Figure 8. Comparison of the posterior effects of (A) water temperature, (B) date, (C) number of traps, and (D) use of modified traps and year on the daily probability of detection of giant gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 2011–2013, using informative (red solid lines) and vague (blue dashed lines) prior probabilities. Bold lines and points represent means; light lines represent 95-percent credible limits.

Discussion

Based on our results, proximity to historical habitat was an important variable for predicting the probability of occurrence of giant gartersnakes at sampled sites in the Sacramento Valley. The effect of historical habitat was evident despite the conversion of nearly all natural marshes to other land uses in the past century (with some subsequent marsh restoration; Garone, 2007). Agricultural wetlands also provided apparently suitable habitat at locations where we did not detect giant gartersnakes (Halstead and others, 2010), and where the current analysis indicated a slightly lower probability of occurrence.

We hypothesize that the relation between distance to historical tule marsh habitat and ψ is caused by dispersal limitations of giant gartersnakes at the scale of the Sacramento Valley. Although habitat alteration has eliminated nearly all natural marsh habitat from the Sacramento Valley (Frayer and others, 1989; Garone, 2007), the occurrence of rice agriculture and its supporting network of irrigation and drainage canals and the restoration of marsh habitats provide much suitable habitat throughout the area of inference (Halstead and others, 2010). Our research indicates, however, that giant gartersnakes have not been able to disperse into all suitable habitats, and are largely restricted to areas near locations at where they likely were historically abundant. It remains to be determined whether an equilibrium status has been reached in agricultural habitats, or whether giant gartersnakes are repaying an "extinction debt" (for example, Tilman and others, 1994).

Another potential mechanism that could cause the relation between distance to historical tule marsh habitat and ψ is extirpation of giant gartersnakes from areas farther from historical tule marsh. Extirpation from areas farther from historical tule marsh could occur if, for example, reclamation of marshes for agriculture or other uses first occurred farther from mapped historical tule marsh, and extirpation is a function of time since conversion, as occurs with extinction debt. Extirpation from these areas also might be facilitated by less connectivity among populations farther from historical marsh, such that as habitats were converted to agriculture and other uses, locations at which giant gartersnakes were extirpated did not have a nearby source of dispersing individuals to recolonize remaining (or created) habitat.

The boundaries and extent of historical marsh habitat were likely more heterogeneous than suggested by the available data. The discrepancy between the true locations of historical marsh and the mapped locations of historical marsh could result in errors in estimating the strength of the relationship between distance to historical marsh and the probability of giant gartersnake occurrence, and errors in predicting the probability of occurrence of giant gartersnakes at a specific location. In particular, islands of upland habitat likely existed within the area mapped as historical marsh, and small marshes undoubtedly existed in areas mapped as California prairie. Indeed, the greatest discrepancy between the mapped probability of occurrence and known independent giant gartersnake locations occurs in the northeastern portion of the giant gartersnake range (figs. 3 and 4). We hypothesize that this discrepancy is caused by the lack of a hard barrier to dispersal into historical marshes embedded in a matrix of historical California prairie. We further hypothesize that closed canopy habitats like historical riparian forest likely constituted a barrier to giant gartersnake dispersal, resulting in their absence from areas otherwise mapped as suitable by Halstead and others (2010). A larger sample of sites will be required to evaluate these more complex hypotheses representing a more nuanced view of giant gartersnake occurrence.

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The only contemporary habitat variable affecting the probability of occurrence of giant gartersnakes was the proportion cover of submerged vegetation. Direct effects of submerged vegetation were not evident; rather, the effect of submerged vegetation on ψ was affected by distance to historical marsh. At locations in or near areas that historically were marsh habitat, greater submerged vegetation was related to a lower probability of occurrence. This relation was reversed at greater distances to historical marsh. We hypothesize that this was the result of two factors. First, thick cover of submerged vegetation can obstruct waterways, potentially impeding locomotion or foraging efficiency of giant gartersnakes, or by decreasing the abundance of prey, resulting in a reduced probability of occurrence of giant gartersnakes. At greater distances from historical marsh, however, submerged vegetation might indicate more permanent water features that might allow dispersing giant gartersnakes, or those populations persisting in historical isolated marshes distant from mapped historical marsh, to persist. Alternatively, the positive relation of ψ with submerged vegetation cover at greater distances to historical marsh could be an artifact of low sample size. No sites distant from historical marsh had a high proportion of submerged vegetation, but one occupied site was a moderate distance from historical marsh and had moderate amounts of submerged vegetation. This site likely was influential in the model, given the relatively small sample size involved. Regardless of the mechanism leading to our results, the maximum percent cover of submerged vegetation was 12.8 percent; in areas near historical marsh where giant gartersnakes are likely to occur, even this moderate amount of submerged vegetation apparently was enough to result in a reduced probability of occurrence.

Although other habitat and vegetation conditions were not determined to be important at the landscape scale considered here, this does not mean that these variables are unimportant. The effect of existing habitat conditions likely operates on small spatial scales, where dispersal limitations are less important. Indeed, the effects of current habitat conditions on ψ likely are conditional on the opportunity for a population to have become established at a location. With larger sample sizes, additional interactions between distance to historical marsh and other habitat or vegetation variables likely would be supported. Larger sample sizes also would reduce the likelihood of spurious results or provide stronger confirmation of the results of this study.

In addition to habitat variables, relative fish count also was negatively related to the probability of occurrence of giant gartersnakes. Because fish are important prey for giant gartersnakes, this finding was unexpected. Our measure of relative fish count was bycatch in traps, and, therefore, represents size classes of fish available as prey to giant gartersnakes. Several possible mechanisms might have led to our results. Some small potential prey fish could escape from funnel traps, giving a false representation of fish abundance at study sites. Another possibility is that a greater number of small fish in traps, particularly centrarchid species, might indicate a greater abundance of larger fish that prey on giant gartersnakes. There might be a threshold of fish abundance or size distribution that changes predator-prey interactions between giant gartersnakes and these fish species. Alternatively, fewer fish where probability of occurrence is higher might indicate depletion of fish prey (at least within traps) where giant gartersnakes occur. Additional studies will be necessary to resolve which of these mechanisms (or others) might have caused the observed pattern.

In many ways, prey counts operate in a manner similar to that of microhabitat and local vegetation conditions—prey counts likely only matter within or near the historical range of giant gartersnakes, where populations are or could readily become established, and are less likely to have been extirpated. Although prey are necessary for predators to persist, and are related to ψ for some aquatic snake species (Durso and others, 2011), all sampled wetlands had fish of appropriate size to be consumed by giant gartersnakes, and most also had tadpoles and frogs. As for local habitat variables, directed studies at small spatial scales within the historical range of giant gartersnakes will be necessary to evaluate how prey abundance affects the distribution of giant gartersnakes.

Detection probabilities of giant gartersnakes were relatively low, but within the range of values observed for other aquatic snakes (Durso and others, 2011). Informative priors improved inference about the precision of the effects of covariates on p, but had little effect on posterior inference about ψ. The greatest effect of using informative priors was to decrease model selection uncertainty, which was substantial even with informative priors. We had expected that the greater precision offered by informative priors would have improved inference ψ. We suspect that inference about the probability of occurrence of giant gartersnakes was unchanged by placing informative priors on the detection component of the model because:

1. Priors were consistent with the observed data;
2. The number of sites was small, limiting the posterior precision of occupancy parameter estimates; and
3. p was low enough (even when estimated more precisely) that substantial uncertainty remained about the occurrence status of giant gartersnakes at sites where the species was undetected.

Many variables other than distance from historical tule marsh and relative fish count likely affect the probability of occurrence of giant gartersnakes at the landscape scale. The greatest limitation of our study was the small number of sampled sites. We initially incorporated a removal design to accommodate a larger sample of sites under the assumption that informative priors would help to alleviate the loss of information about p inherent in the removal design (MacKenzie and Royle, 2005). The greatest limitation to sample size was not the amount of time or number of surveys required at each site, however, but difficulty obtaining permission to sample on private land. Most of our area of inference was on private land, but we were able to sample some locations on public lands as part of our random selection of sites. Although many landowners were very cooperative, some did not return calls or denied permission outright. Thus, although our study design was intended to increase the number of randomly selected sites sampled, we were unable to fully realize its potential. Site selection was not truly random because all sampling was contingent on landowner permission. Because of difficulty in obtaining permission and the resulting small sample size, in 2013 we abandoned random site selection in

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an attempt to increase the number of sampled sites, but we still met with limited success obtaining permission to sample sites. The primary limitations related to our small sample of sites were:

1. Increased model selection uncertainty,
2. Imprecise estimation of ψ and the strength of the effects of variables on ψ, and
3. Limitation of the number of variables (and interaction terms) included in the models.

Nonetheless, our study provides information about which variables affect the contemporary distribution of giant gartersnakes at sampled sites in the rice-growing regions of the Sacramento Valley.

Single-season occupancy models require the assumption that sites are closed to changes in presence or absence. More specifically, the closure assumption applies across the repeat surveys within a site, and violation of this assumption will tend to bias p low and ψ high (Rota and others, 2009). Our sampling scheme, which was for 21 or fewer consecutive days of sampling within a site, likely met the closure assumption for giant gartersnakes at sampled sites. Lack of closure at sampled sites for the three-year duration of the study would be unlikely to result in bias, unless a large portion of sampled sites tended to have higher or lower probabilities of occurrence during the year that site was sampled relative to the years that were not sampled. It is difficult to imagine a mechanism that would cause such a scenario. The effects of variables also should have been unaffected by the three-year sampling duration of the project, because covariates were measured at the time of sampling, and therefore applied to the occurrence status of sites at that time. The exception to this would have been for GIS-derived variables, which were static in time, but (except for distance to historical marsh) subject to change. Wholesale changes in the location and extent of rice agriculture, wetlands, and canal density did not appear to have changed appreciably among the years of our study.

Information about how the probability of occurrence of giant gartersnakes varies throughout the Sacramento Valley is important information for managing water transfers based on rice land idling. Preliminary results suggest that actions that have the potential to negatively affect giant gartersnakes near historical tule marsh might have more adverse consequences for giant gartersnakes than similar actions taken farther north and toward the edges of the Sacramento Valley. The potential effects of water transfers on giant gartersnakes, particularly transfers occurring in areas that historically were marsh habitat, will be explored further.

Given the historical inability of giant gartersnakes to disperse into apparently otherwise suitable habitat, or to be extirpated from these regions and fail to recolonize, presents concerns regarding the ability of giant gartersnakes to relocate to more suitable habitat in response to altering of habitat such as rice land idling. This result also suggests that restoration efforts located far from historical marsh might require accompanying translocation of giant gartersnakes to establish populations at these sites. The mobility of giant gartersnakes in response to rice land idling for the purpose of water transfers will need to be evaluated further. The science needed to inform effective conservation of species inhabiting highly altered landscapes will need to look forward to future challenges, while also looking back to examine the ecological limitations affecting these species.

Summary

- We examined the occurrence of giant gartersnakes in rice growing regions of the Sacramento Valley, California.
- Detection probabilities were low, but trap modifications incorporated in 2012 and 2013 were effective at increasing detection probabilities by about 600 percent.
- Substantial model selection uncertainty existed, but we found a consistent negative effect of distance to historical tule marsh on the probability of occurrence of giant gartersnakes.
- Occurrence of giant gartersnakes also was explained by an interaction between distance to historical habitat and proportion submerged vegetation present in the contemporary habitat. A negative effect of submerged vegetation was evident in areas in or near historical tule marsh, but this relation was reversed (and more uncertain) as distance from historical tule marsh increased.
- Relative fish count negatively affected probability of occurrence of giant gartersnakes, although the underlying reason for this result is unclear.
- Additional study with a larger sample of sites would help to further resolve the distribution of giant gartersnakes in the Sacramento Valley, including those variables that affect where giant gartersnakes occur.

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Glossary

Abundance: The number of individual organisms in a population.

Anuran: Any amphibian of the order Anura, comprising the frogs and toads.

Body condition: Any of a number of indices that relate body mass to structural body size.

Brumation: The dormant, hibernation-like state that ectothermic animals use during cold weather.

Centrarchidae: A family of North American freshwater ray-finned fishes belonging to the order Perciformes; includes black basses and sunfishes.

Cloaca: The common cavity into which the intestinal, genital, and urinary tracts open in birds, reptiles, amphibians, many fishes, and monotremes.

Colonization: The process of establishment of organisms of a species in a new location.

Convergence: In Markov chain Monte Carlo simulations, the state of having reached the stationary posterior distribution.

Credible Interval (Limits): In Bayesian statistics, the domain of a posterior probability distribution that represents the specified level of uncertainty. For example if the probability that the value of a parameter, say ψ, lies between 0.45 and 0.65 is 0.95, then $0.45 \leq \psi \leq 0.65$ is a 95% credible interval of ψ, and 0.45 and 0.65 are the 95% credible limits.

Cyprinidae: A large family of freshwater fishes including the carps, the true minnows, and their relatives.

Demography: The study of populations, particularly changes over time in populations.

Density: The quantity of a substance per unit space. In ecology, the number of individuals in a population per unit area.

Detection probability: The probability that one or more individuals of a species is detected in a survey, given that the species is present at the location surveyed.

Dimorphic: Having two forms.

Dispersal: The spread of organisms to new areas.

Endemic: Native to a specific region or environment and not occurring naturally anywhere else.

Extinction debt: The future extinction of species caused by events in the past. Extinction debt occurs because of time delays between negative effects on a species and the species' ultimate disappearance.

Extirpate: To cause a species (or other taxon) to cease to exist in a geographic area, although it still exists elsewhere.

Gravid: Pregnant.

Hemipenis: One of a pair of intromittent organs of male squamates (snakes, lizards, and worm lizards).

Microhabitat: An extremely localized, small-scale environment.

Natricine: Any of a member of a subfamily of the Colubridae family of snakes that comprises 28 genera; includes gartersnakes and watersnakes.

Neonate: A newborn.

Obligate: Restricted to a certain condition of life.

Occupancy: The act, state, or condition of a species living at a site.

Parturition: The process of bringing forth young.

Posterior (probability distribution): In Bayesian statistical inference, the probability distribution of an unknown quantity, treated as a random variable, conditional on the evidence obtained from an experiment or survey.

Precinctive: A species (or smaller taxonomic unit) that is restricted to a defined geographical area.

Prior (probability distribution): In Bayesian statistical inference, the probability distribution that expresses one's belief about an uncertain quantity before some evidence is taken into account.

Removal design: An occupancy survey design where sites are surveyed up to a maximum number of times, but surveying stops at a site once the species is detected.

Subspecies: A subdivision of a species, especially a geographical or ecological subdivision.

Take: To harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or engage in any such conduct.