

Ghost of habitat past: historic habitat affects the contemporary distribution of giant garter snakes in a modified landscape

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Abstract

Historic habitat conditions can affect contemporary communities and populations, but most studies of historic habitat are based on the reduction in habitat extent or connectivity. Little is known about the effects of historic habitat on contemporary species distributions when historic habitat has been nearly completely removed, but species persist in a highly altered landscape. More than 93% of the historic wetlands in the Central Valley of California, USA, have been drained and converted to agricultural and other uses, but agricultural wetlands, such as rice and its supporting infrastructure of canals, allow some species to persist. Little is known about the distribution of giant garter snakes *Thamnophis gigas*, a rare aquatic snake species inhabiting this predominantly agricultural landscape, or the variables that affect where this species occurs. We used occupancy modeling to examine the distribution of giant garter snakes at the landscape scale in the Sacramento Valley (northern portion of the Central Valley) of California, with an emphasis on the relative strength of historic and contemporary variables (landscape-scale habitat, local microhabitat, vegetation composition and relative prey counts) for predicting giant garter snake occurrence. Proximity to historic marsh best explained variation in the probability of occurrence of giant garter snakes at the landscape scale, with greater probability of occurrence near historic marsh. We suspect that the importance of distance to historic marsh represents dispersal limitations of giant garter snakes. These results suggest that preserving and restoring areas near historic marsh, and minimizing activities that reduce the extent of marsh or marsh-like (e.g. rice agriculture, canal) habitats near historic marsh may be advantageous to giant garter snakes.

Introduction

Historic habitat conditions can affect contemporary communities and populations in several ways. In perhaps the most common situation, widespread habitats are reduced to small fragments or once large habitat patches are reduced in size, decreasing connectivity among and abundance within population subunits (Lindborg & Eriksson, 2004; Herben *et al.*, 2006). The persistence of species in these small fragments can represent an 'extinction debt' (Tilman *et al.*, 1994) whereby the species is present, but positive population growth cannot be sustained and extirpation is imminent. This lagged effect of habitat alteration on species persistence results in inflated values of patch occupancy and species richness because an equilibrium subsequent to the disturbance has not yet been achieved (Sang *et al.*, 2010).

Most studies of historic habitat conditions on communities and populations have focused on changes in species richness, patterns of occupancy and demography in remnants of once widespread habitats (Lindborg & Eriksson,

2004; Herben *et al.*, 2006; Piha, Luoto & Merilä, 2007; Sang *et al.*, 2010). For wetland species precinctive to the Central Valley of California, USA, where wetlands have been reduced in extent from more than 10 000 km² to less than 650 km² (a reduction of more than 93%) over the past 150 years (Frayser, Peters & Pywell, 1989; Garone, 2007; Huber, Greco & Thorne, 2010), remnant natural wetlands are nearly nonexistent. Water diversion and flood protection programs in the early 20th century resulted in a highly modified agricultural landscape in which water is tightly controlled. Contemporary wetlands are largely agricultural, consisting of rice fields and their associated supporting infrastructure of canals and drains. Thus, the historic distribution of wetland habitats, particularly tule marshes, and the distribution of current agricultural wetlands are not necessarily congruent.

Despite the massive loss of wetland habitat and intensive agriculture in the Central Valley, some species, such as giant garter snakes *Thamnophis gigas*, persist in highly modified agricultural wetlands. Giant garter snakes compose an

aquatic snake species precinctive to the Central Valley, where they historically occurred in marshes, sloughs and other habitats with slow-moving, relatively warm water and emergent vegetation (Fitch, 1940; Hansen & Brode, 1980). Giant garter snakes are state-listed and federally listed as threatened (California Department of Fish and Game Commission, 1971; US Fish and Wildlife Service, 1993) because of habitat loss, and they have been nearly extirpated from the San Joaquin Valley (southern portion of the Central Valley). Populations of giant garter snakes still persist in the rice agricultural regions of the Sacramento Valley (northern portion of the Central Valley; Halstead, Wylie & Casazza, 2010).

Our primary goal was to examine whether historic habitat or contemporary conditions were better predictors of the distribution of a species in a highly modified landscape. As a case study, we examined the distribution of giant garter snakes in the Sacramento Valley of California. We expected that habitat conditions most nearly resembling tule marsh habitats (high proportion of cover of emergent vegetation, dominated by tules *Schoenoplectus acutus*, with abundant fish and amphibian prey) would have greater probabilities of occurrence of giant garter snakes. We further expected that locations closer to historic tule marsh habitat would be more likely to be occupied by giant garter snakes. We therefore compared the strength of evidence for the effects of historic and contemporary landscape variables, current local habitat composition, current local vegetation composition and current prey counts on the probability of occurrence of giant garter snakes.

Methods

Study site

Our study area was an approximately 7500 km² area encompassing five recovery units for giant garter snakes outlined in the draft Recovery Plan for the Giant Garter Snake (US Fish and Wildlife Service, 2011). We overlaid a 5 × 5-km grid over the study area, and selected grid cells in which to sample at random, stratified by recovery unit. Grid cells were only included in the sampling frame if they contained at least 1 contiguous ha of rice agriculture or (restored) marsh habitat that is potentially suitable for occupancy by giant garter snakes (Halstead *et al.*, 2010), resulting in the selection of 46 out of the possible 294 potential grid cells. The potential area that could be sampled in recovery units ranged from *c.* 500 to 2500 km², and we selected between 4 and 17 grid cells per recovery unit in direct proportion to the number of grid cells available in each recovery unit. Most selected grid cells occurred on private land, so we used plat map software (ParcelQuest; <http://www.parcelquest.com>) to identify landowners and obtain contact information. We contacted landowners for permission and moved on to other landowners within each grid cell until all landowners whose property contained appropriate habitat [rice agriculture and associated canals or wetlands; permanent (or near permanent) water was a requirement for sampling] in each grid cell

were contacted. Several landowners denied permission; many more did not return repeated calls or e-mails. Sampled sites therefore consisted of locations in or immediately adjacent to selected grid cells where landowner permission was obtained. Five of the sites were not selected purely at random, but were located where partner agencies desired surveys. We had no prior knowledge of the occurrence status of giant garter snakes at each of these locations. In total, we obtained permission to sample 16 sites in 2011 and eight sites in 2012, with sites spread throughout the Sacramento Valley.

Field methods

We sampled aquatic habitats in selected sites using floating funnel traps (Casazza, Wylie & Gregory, 2000). In 2011, we sampled sites between 18 May and 28 September, and in 2012 we sampled sites between 8 June and 14 September. To sample each site, we deployed 100 traps spaced 5–10 m apart in one or more transects of 25–100 traps each (transect length = 125–1000 m), although we sampled three sites with 50 traps because of limited available trappable habitat. In 2011, we used a removal design, whereby we deployed traps for up to 21 consecutive days or until a giant garter snake was captured. The duration of sampling sites in 2011 therefore varied from 2 to 21 (mean = 16) consecutive days. Because we modified traps with one-way entrances in 2012 (Halstead, Wylie & Casazza, 2013), we did not use a strict removal design that year to provide more information about the effects of trap modifications on the detection process. The duration of sampling each site in 2012 varied from 5 to 29 (mean = 19) consecutive days. We marked, measured and sexed each captured individual giant garter snake, and released individuals at their location of capture immediately after processing.

We characterized contemporary microhabitat and vegetation composition associated with the sampled locations at each site. At each trap location, we visually estimated the percentage cover of microhabitats (open water, submerged vegetation, emergent vegetation, floating vegetation, terrestrial vegetation, litter, bare ground and rock) within a 1-m radius of each trap. Because our traps are intentionally placed at habitat edges, we also collected habitat data at a random location selected from a discrete uniform distribution between 2 and 5 m to the left of odd-numbered traps as trap number increased along the transect (we numbered traps consecutively at each transect), and to the right of even-numbered traps as trap number increased along the transect, again using a circle with 1-m radius. Incorporating the random points into the analysis provided information about the aquatic and terrestrial environments immediately adjacent to the transect, rather than characterizing only the sampled habitat edges. Within these same circular quadrats, we also visually estimated the percentage cover of vegetation types [tule, cattail (*Typha* spp.), water primrose (*Ludwigia* spp.), mosquito fern (*Azolla* spp.), duckweed (*Lemna* spp.), algae, Cyperaceae, Juncaceae, pondweed

(*Potamogeton* spp.), knotweed (*Polygonum* spp.), Poaceae, forbs, shrubs/vines and cultivated rice (*Oryza sativa*).

We also characterized relative prey counts at sampled locations within each site. At every fifth trap on each transect, we counted the number of nontarget species [anurans (larvae and adults), fish (by family), crayfish, insects and other species] in each trap. We emptied traps in which nontarget species were counted daily, but left potential prey in other traps to serve as natural bait.

Analytical methods

We used single-season occupancy models (MacKenzie *et al.*, 2002, 2006; Kéry, 2010; Kéry & Schaub, 2011) to examine the patterns in the probability of occurrence (ψ) of giant garter snakes in the Sacramento Valley. Because of our small sample size, we evaluated four different model sets for the covariates of ψ : (1) contemporary and historic variables available in a geographic information system (GIS) that could be used to predict patterns of giant garter snake occurrence across the landscape; (2) site-specific microhabitat characteristics (as a measure of habitat structure); (3) site-specific vegetation species composition; (4) relative prey counts. In each case, we limited the number of predictor variables to four and did not consider interaction terms.

The GIS variables we examined included proportion rice, proportion wetland, linear canal density and distance to historic tule marsh (Table 1). We chose the proportion habitat and canal density variables because they were most predictive in a previous habitat suitability analysis (Halstead *et al.*, 2010). We calculated proportions and densities within a 2.5-km buffer of each transect. We chose a buffer of 2.5 km because it was similar to our grid cell sizes used in the selection of sites and large enough to meet closure assumptions for giant garter snake populations over the course of a 2-year study. Proportion habitat variables

were digitized based on the US Department of Agriculture 2010 National Agricultural Imagery Program imagery, and canal density was based on the US Geological Survey National Hydrography Dataset. We chose historic tule marsh because it represented likely locations of historically suitable habitat, and we hypothesized that distance to this historic habitat might explain current distribution patterns for giant garter snakes. We calculated the distance from each trap to historic tule marsh (based on Küchler, 1977) using the Near tool in ArcGIS 9.3 (ESRI, 2008). To obtain a site-specific covariate for distance to historic tule marsh, we calculated the mean distance to historic tule marsh across traps within each site.

The four local microhabitat variables we selected were also based on the ecology of giant garter snakes (Table 1). We used the mean proportion of each selected variable calculated across all trap and random locations within a site. We used proportion emergent vegetation because we hypothesized that it would provide cover and foraging locations for giant garter snakes, thereby increasing ψ . Similar logic was used for proportion submerged vegetation, which we expected to provide richer prey communities, and proportion terrestrial vegetation, which would provide basking cover near steep canal or wetland banks. We hypothesized that proportion floating vegetation, which often forms thick mats during the active season (April–September; Wylie *et al.*, 2009), would negatively affect ψ because of its potential negative effects on prey communities, inhibition of locomotion by giant garter snakes or other mechanisms.

We focused on common aquatic vegetation types for the analysis of the effects of vegetation on the occurrence of giant garter snakes (Table 1). As for microhabitat variables, we used the mean proportion of each selected variable calculated across all trap and random locations within a site. We expected proportion tule, the dominant historic marsh vegetation in the Sacramento Valley (Garone, 2007), to be positively related to ψ . Proportion cattail and proportion

Table 1 Summary statistics of site predictor variables used in the analysis of giant garter snake (*Thamnophis gigas*) occurrence in the rice-growing regions of the Sacramento Valley, 2011–2012

Model set	Variable	Mean	SD	Range
GIS	Proportion rice	0.571	0.204	0.121–0.932
	Proportion wetland	0.143	0.133	0.000–0.424
	Distance to historic marsh	8.312	10.321	0.00–35.087
	Canal density	13.416	5.962	1.788–25.308
Microhabitat	Proportion emergent vegetation	0.221	0.160	0.001–0.568
	Proportion submerged vegetation	0.012	0.028	0.000–0.128
	Proportion floating vegetation	0.075	0.093	0.000–0.334
	Proportion terrestrial vegetation	0.188	0.112	0.026–0.451
Vegetation	Proportion tule	0.086	0.119	0.000–0.428
	Proportion cattail	0.072	0.073	0.000–0.266
	Proportion water primrose	0.113	0.186	0.000–0.689
	Proportion mosquito fern	0.045	0.083	0.000–0.291
Prey	Mean tadpole count per trap per day	0.268	0.628	0.000–2.695
	Mean frog count per trap per day	0.024	0.027	0.000–0.093
	Mean fish count per trap per day	0.287	0.240	0.011–0.959

GIS, geographic information system; SD, standard deviation.

water primrose were similarly expected to increase ψ because of the cover and structure they can provide giant garter snakes. We expected that proportion mosquito fern, which can form dense floating mats, would be negatively related to ψ for the same reasons as total floating vegetation.

We examined three major categories of prey as predictors of giant garter snake occurrence (Table 1). 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 *Lithobates catesbeianus*. We grouped all fishes together for analysis. Fish assemblages at our sites were predominantly introduced species, including mosquito fish *Gambusia* spp., 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 analysis. Although we did not account for potential biases caused by imperfect detectability of prey, we suspect that relative prey counts are a reliable index of the availability of prey for giant garter snakes at sampled sites.

We analyzed all models, which were coupled logistic regressions for predictors of occurrence and detection, using Bayesian methods. We used the same observation model for daily detection probability at each site (p) with each model set. We used variables identified in Halstead *et al.* (2011) 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 2). The use of informative

priors should improve the parameter estimation efficiency of models based on the removal design, which provides less information on the detection process than a balanced study design (Mackenzie & Royle, 2005), but is more efficient in the use of time and resources. Because we used modified traps in 2012, we included a variable for the use of modified traps in the detection model. Unlike other detection variables, we gave modified traps a vague prior distribution because we did not have information on the magnitude of the effect of the trap modification on p (Table 2). 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 2).

We analyzed each occurrence model set separately. We quantified the probability of all subsets of the full additive model for each model set using indicator variables on model coefficients (Kuo & Mallick, 1998; Royle & 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 a model set containing four variables; 0.125 in a model set containing three variables). We used vague *N*(0,1.65) priors, which are approximately uniform on the probability scale (Lunn *et al.*, 2013) for all model coefficients (which are on the logit scale). To examine the effects of our choice of priors, we conducted a prior sensitivity analysis using vague *N*(0,10) priors for all model coefficients with informative priors on detection model coefficients. We standardized all predictor variables to mean zero and unit variance prior to analysis. We calculated

Table 2 Priors for model parameters. Normal distributions are given as *N*(mean, standard deviation)

Model component	Model set	Parameter	Symbol	Prior probability	
				Informative	Vague
Detection	All	Intercept	α_0	<i>N</i> (-2.02, 0.133)	<i>N</i> (0, 1.65)
		Effect of water temperature	α_{wt}	<i>N</i> (0.277, 0.052)	<i>N</i> (0, 1.65)
		Effect of date	α_{date}	<i>N</i> (-0.307, 0.059)	<i>N</i> (0, 1.65)
		Effect of number of traps	α_{ntrap}	<i>N</i> (0.321, 0.118)	<i>N</i> (0, 1.65)
		Effect of trap modification	α_{tm}		<i>N</i> (0, 1.65)
		Random site effect	ϵ_{site}	<i>Gamma</i> (100.4, 98.5)	<i>Uniform</i> (0, 10)
Occurrence	All	Intercept	β_0		<i>N</i> (0, 1.65)
	GIS	Effect of proportion rice	β_{rice}		<i>N</i> (0, 1.65)
		Effect of proportion wetland	β_{wet}		<i>N</i> (0, 1.65)
		Effect of distance to historic marsh	β_{hm}		<i>N</i> (0, 1.65)
		Effect of linear canal density	β_{canal}		<i>N</i> (0, 1.65)
		Local habitat	Effect of proportion-emergent vegetation	β_{ev}	
		Effect of proportion-submerged vegetation	β_{sv}		<i>N</i> (0, 1.65)
		Effect of proportion-floating vegetation	β_{fv}		<i>N</i> (0, 1.65)
		Effect of proportion terrestrial vegetation	β_{tv}		<i>N</i> (0, 1.65)
	Local vegetation	Effect of proportion tule	β_{tule}		<i>N</i> (0, 1.65)
		Effect of proportion cattail	β_{ct}		<i>N</i> (0, 1.65)
		Effect of proportion water primrose	β_{vp}		<i>N</i> (0, 1.65)
		Effect of proportion mosquito fern	β_{mf}		<i>N</i> (0, 1.65)
	Prey	Effect of tadpole count	β_{tad}		<i>N</i> (0, 1.65)
		Effect of frog count	β_{frog}		<i>N</i> (0, 1.65)
Effect of fish count		β_{fish}		<i>N</i> (0, 1.65)	

GIS, geographic information system.

model-averaged posteriors for parameters across the entire model set, using a value of zero if the parameter was not included in the model. Posterior inference was based on five chains of 200 000 iterations each, after a burn-in period of 100 000 iterations. We thinned each chain by a factor of 100, keeping 10 000 iterations to describe the posterior distribution of each parameter. We analyzed each model with OpenBUGS 3.2.2 (Lunn *et al.*, 2009) called from R 2.15.2 (R Core Team, 2013) using the package R2OpenBUGS (Sturtz, Ligges & Gelman, 2005). We diagnosed convergence with visual examination of history plots and with the Gelman–Rubin statistic (Gelman & Rubin, 1992); no evidence for lack of convergence was observed.

Results

We detected giant garter snakes at 11 of 24 sampled sites. For the GIS-level analysis, models containing an effect of distance to historic tule marsh had the greatest support from the data, but considerable model selection uncertainty existed (Table 3). The posterior probability of an effect of historic tule marsh on ψ was 0.840 with informative priors (0.804 with vague priors); the null model had a posterior probability of only 0.055 with informative priors (0.051 with vague priors; Table 3). Using $N(0,10)$ vague priors on model coefficients decreased model selection uncertainty and increased the posterior probability of the null model [posterior probability of an effect of historic tule marsh = 0.680; posterior probability of best model (effect of historic tule marsh only) = 0.402; posterior probability of null model = 0.244]. The model-averaged posterior distribution of the effect of distance to historic marsh (β_{hm}) using informative priors was -1.26 (95% confidence interval = -3.068 – 0.000 ; Fig. 1). Inference about β_{hm} was unaffected by the use of informative priors on detection parameters [β_{hm} with vague priors = -1.27 (-3.29 – 0.00)]. In general, ψ was greatest along the center of the floor of the

Sacramento Valley and decreased to the north and toward the edges of the valley (Fig. 2).

For the model set based on local microhabitat conditions, the null model had the greatest posterior probability (0.191 with informative priors; 0.154 with vague priors; Table 4). The null model had even greater posterior probability (0.649) under alternative $N(0,10)$ priors on model coefficients. Considerable model selection uncertainty existed, but model-averaged 95% credible intervals for all parameters fully contained zero.

For the model set based on local vegetation composition, the model with an effect of proportion water primrose (β_{wp}) on ψ had the greatest posterior probability (0.200); the null model was ranked second with a posterior probability of 0.182 (Table 5). The ranking of the null and water primrose models was reversed when vague priors were used (posterior probabilities 0.154 and 0.148, respectively). These posterior model probabilities were 0.571 for the null model and 0.228 for the water primrose effect only model under alternative $N(0,10)$ priors. Although it appeared in four of the top six models based on informative priors, the model-averaged posterior distribution of β_{wp} fully contained zero [-0.075 – 2.505]. Inference about β_{wp} was unaffected by the use of informative priors [β_{wp} with vague priors = 0.495 (-0.205 – 2.618)]. As with the GIS-level and local microhabitat analyses, considerable model selection uncertainty existed among the models comprising the vegetation composition model set.

For the model set based on mean prey counts, the null model had the greatest posterior probability when informative priors were used (0.297), but the model with an effect of

Table 3 Model selection results for occupancy of giant garter snakes *Thamnophis gigas* in the Sacramento Valley, California, 2011–2012, based on landscape variables derived from GIS

Parameter				Posterior probability	
β_{rice}	β_{wet}	β_{hm}	β_{canal}	Informative	Vague
0	0	1	0	0.272	0.214
0	1	1	0	0.163	0.123
1	0	1	0	0.104	0.099
0	0	1	1	0.091	0.112
1	1	1	0	0.072	0.075
0	1	1	1	0.065	0.073
0	0	0	0	0.055	0.051
1	0	1	1	0.042	0.065

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 the null model and models with a greater posterior probability than prior probability (0.063) are shown. GIS, geographic information system.

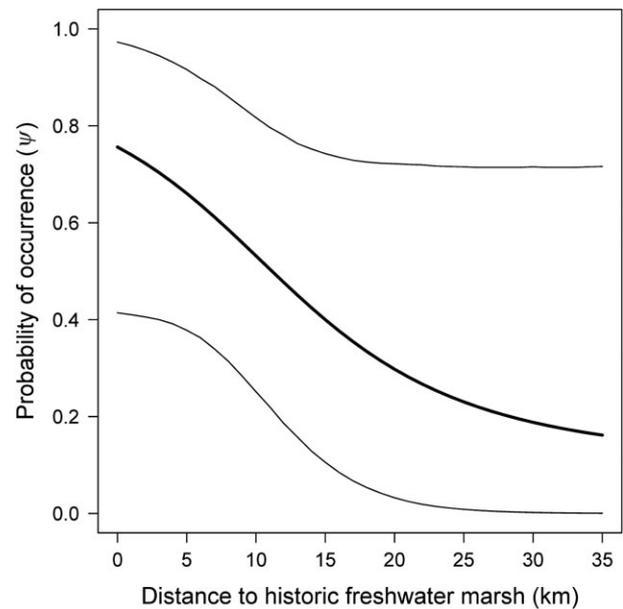


Figure 1 Model-averaged effect of the distance to historic tule marsh on the probability of occurrence of giant garter snakes *Thamnophis gigas* in the rice-growing regions of the Sacramento Valley, California, 2011–2012.

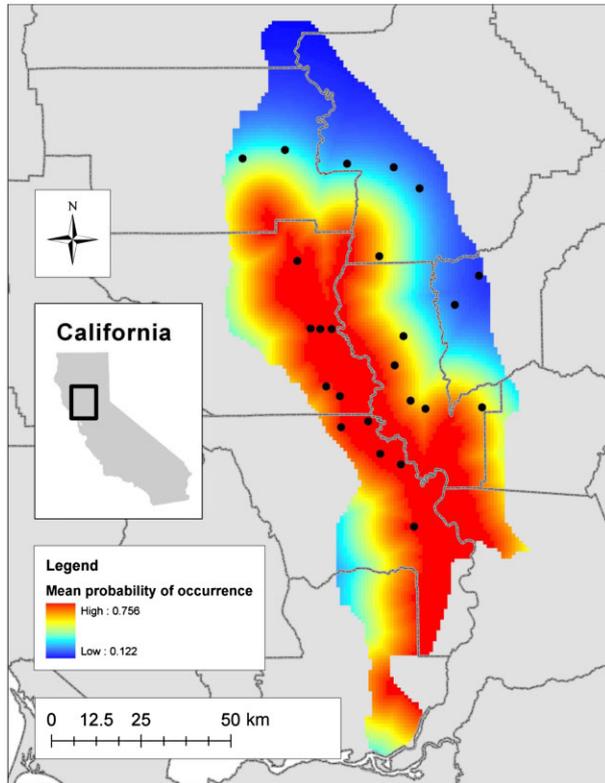


Figure 2 Model-averaged probability of occurrence of giant garter snakes *Thamnophis gigas* in the rice-growing regions of the Sacramento Valley, California, 2011–2012, based on the geographic information system-level model set. Black dots indicate sampling locations.

Table 4 Model selection results for occupancy of giant garter snakes *Thamnophis gigas* in the Sacramento Valley, California, 2011–2012, based on local microhabitats

Variable				Posterior probability	
β_{ev}	β_{sv}	β_{rv}	β_{rv}	Informative	Vague
0	0	0	0	0.191	0.154
0	1	0	0	0.170	0.162
1	0	0	0	0.080	0.084
1	1	0	0	0.080	0.083
0	1	1	0	0.079	0.080
0	0	1	0	0.069	0.070
0	1	0	1	0.069	0.065

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 (0.063) are shown.

fish counts (β_{fish}) was highest ranked with vague priors (0.231; Table 6). As with other model sets, using alternative $N(0, 10)$ priors on model coefficients increased the posterior probability of the null model to 0.586 and decreased the posterior probability of the fish effect model to 0.217. In both former cases, the model-averaged posterior

Table 5 Model selection results for occupancy of giant garter snakes *Thamnophis gigas* in the Sacramento Valley, California, 2011–2012, based on local vegetation composition

Parameter				Posterior probability	
β_{tule}	β_{ct}	β_{vp}	β_{mf}	Informative	Vague
0	0	1	0	0.200	0.148
0	0	0	0	0.182	0.154
1	0	1	0	0.078	0.070
1	0	0	0	0.074	0.077
0	0	1	1	0.074	0.065
0	1	1	0	0.074	0.066
0	1	0	0	0.065	0.072
0	0	0	1	0.059	0.065

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 (0.063) are shown.

Table 6 Model selection results for occupancy of giant garter snakes *Thamnophis gigas* in the Sacramento Valley, California, 2011–2012, based on mean counts of potential prey species in traps

Parameter			Posterior probability	
β_{rad}	β_{frog}	β_{fish}	Informative	Vague
0	0	0	0.297	0.208
0	0	1	0.236	0.231
0	1	0	0.128	0.109
0	1	1	0.096	0.132

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 (0.125) are shown.

distribution of β_{fish} fully contained zero [−0.368 (−2.125–0.190) with informative priors; −0.579 (−3.11–0.868) with vague priors]. Considerable model selection uncertainty existed, and model-averaged 95% credible intervals for all parameters fully contained zero.

Not surprisingly, 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. 3). 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. 3). 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. 3). Under average conditions, posterior mean p during our study was 0.116 (0.091–0.144) based on informative priors and 0.159 (0.019–0.516) based on vague priors. Based on informative priors, the use of modified traps in 2012 increased the odds of detection to 7.29 (2.21–18.08) times that of unmodified traps (Fig. 3). The use of vague priors resulted in much greater uncertainty

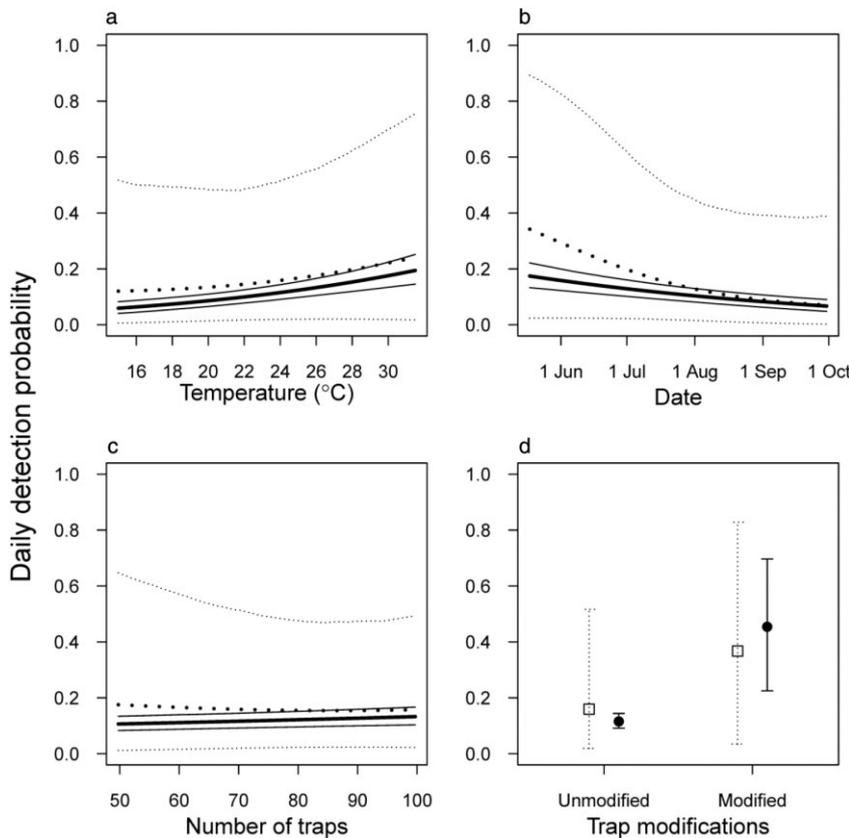


Figure 3 Comparison of the posterior distribution of effects of (a) water temperature, (b) date, (c) number of traps and (d) use of modified traps on the average daily probability of detection of giant garter snakes *Thamnophis gigas* in the Sacramento Valley, 2011–2012, using informative (solid lines) and vague (dotted lines) prior probabilities. Bold lines and points represent posterior means; light lines represent 95% credible limits.

about the effect of trap modifications, with odds of detection 6.41 (0.31–26.93) times that of unmodified traps (Fig. 3).

Discussion

Based on our results, proximity to historic habitat is the most important variable for predicting the probability of occurrence of giant garter snakes in the Sacramento Valley at the landscape scale. The effect of historic habitat was evident despite the conversion of nearly all natural marshes to rice agriculture within the past century (with some subsequent marsh restoration; Garone, 2007). Agricultural wetlands apparently also provided suitable habitat (Halstead *et al.*, 2010) at locations where we did not detect giant garter snakes and where the current analysis indicated a low probability of occurrence. Our study differs from most other studies of the effects of historic habitat on communities and populations because very little unmodified habitat occurs in our study area, and all of our sampling occurred in habitats that have been modified, at least at some point in their history, for agricultural use. We are also unaware of studies of the effects of historic landscape variables on the contemporary distribution of reptiles, although historic habitat connectivity was found to affect amphibian species richness and occupancy on the Swedish island of Gotland (Piha *et al.*, 2007).

We suspect that the relationship between distance to historic tule marsh habitat and ψ is caused by dispersal limitations of giant garter snakes at the scale of the Sacramento Valley. Although habitat alteration has eliminated nearly all natural marsh habitat from the Sacramento Valley (Frayer *et al.*, 1989; Garone, 2007; Huber *et al.*, 2010), the occurrence of rice agriculture, its supporting network of irrigation and drainage canals, and the restoration of marsh habitats currently provide suitable habitat throughout the area of inference (Halstead *et al.*, 2010). Our research demonstrates, however, that giant garter snakes have not been able to disperse into all suitable habitats, and are largely restricted to areas near locations at which they were likely historically abundant. It remains to be determined whether an equilibrium status has been reached in agricultural habitats or whether giant garter snakes are repaying an ‘extinction debt’ (Tilman *et al.*, 1994).

Although current habitat conditions were not found to be important at the landscape scale considered here, this does not mean that they do not affect giant garter snake biology. The effect of current habitat conditions likely operates on smaller spatial scales, where dispersal limitations are less important. Indeed, the effects of current habitat conditions on ψ are likely conditional on the opportunity for a population to have become established at a location. Our sample size was too small to consider more complex models that allowed for interactions between variables, and the spatial

scale of our sampling was likely too coarse to detect the effects of local microhabitat or vegetation conditions, given the great importance of distance to historic tule marsh (i.e. microhabitat and vegetation conditions likely matter in areas near historic tule marsh, but become irrelevant in areas far from historic tule marsh). These issues could be exacerbated by our sampling method, which is only applicable to aquatic habitats. We do not think that the latter is the case, however, because radio telemetry data suggest that giant garter snakes rarely move more than a few meters from aquatic habitats during the active season (G. Wylie, unpubl. data).

Prey counts similarly had little effect on ψ at the landscape scale considered here. In many ways, prey counts operate in a similar manner to microhabitat and local vegetation conditions: prey counts likely only matter within or very close to the historic range of giant garter snakes, where populations are or could readily become established. Although prey are necessary for predators to persist and are related to ψ for some aquatic snake species (Durso, Willson & Winne, 2011), all of our wetlands had fish of appropriate size to be consumed by giant garter snakes, and most also had both tadpoles and frogs in addition to fish. Within these broad taxonomic categories, however, it is unknown to what degree giant garter snakes are selective of potential prey species. Although our study did not account for imperfect detectability of prey, relative prey counts are likely a reliable index of the quantity of prey available to giant garter snakes at sampled sites. As for local habitat variables, directed studies at smaller spatial scales within the historic range of giant garter snakes will be necessary to elucidate how prey abundance affects the distribution, habitat use and population dynamics of giant garter snakes.

Detection probabilities of giant garter snakes were relatively low but within the range of values observed for other aquatic snakes (Durso *et al.*, 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 about occurrence. We suspect that inference about the probability of occurrence of giant garter snakes was unchanged by placing 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; (3) p was low enough (even when estimated more precisely) that substantial uncertainty remained about the status of giant garter snakes at sites where the species was undetected.

Many variables other than distance from historic tule marsh likely affect the probability of occurrence of giant garter snakes on the landscape scale. Perhaps the greatest limitation of our study is the small sample size. We initially incorporated a removal design to accommodate a larger sample of sites with limited resources under the assumption

that informative priors would help to alleviate the loss of information about p inherent in the removal design (MacKenzie & Royle, 2005). The greatest limitation to sample size was not the amount of time or number of samples required at each site, however, but difficulty obtaining permission to sample on private land. Most of our desired area of inference was privately owned, although we were able to sample some locations on public lands as part of our random selection of sites. Although our study design was intended to be random and increase the number of sites sampled, we were unable to fully realize its potential. The primary limitations resulting from our small sample of sites were (1) increased model selection uncertainty; (2) imprecise estimation of ψ and the strength of the effects of covariates on ψ ; (3) limitation of the number of variables (and interaction terms) that could simultaneously be included in the model. Nonetheless, our study is the first to provide valuable information about how historic habitat conditions affect the contemporary distribution of giant garter snakes in the Sacramento Valley, and to our knowledge is the only study evaluating the effects of historic habitat conditions on the contemporary distribution of a reptile.

Information about how the probability of occurrence of giant garter snakes varies throughout the Sacramento Valley is important for resource managers. Actions that degrade or eliminate habitat in the south-central portion of the valley near historic tule marsh are likely to have more serious consequences for the persistence of giant garter snakes than actions taken farther north and toward the edges of the valley. Conversely, habitat restoration projects near locations with higher ψ are more likely to be naturally colonized by giant garter snakes than those near locations with lower ψ . Given the apparent inability of giant garter snakes to disperse into otherwise suitable habitat, it is unlikely that giant garter snakes will be able to adapt to a changing climate by natural dispersal. Likewise, dispersal limitations are likely to have important consequences for conservation of giant garter snakes in the San Joaquin Valley (southern portion of the Central Valley), where widespread extirpation of giant garter snakes occurred following conversion of San Joaquin Valley wetlands to agriculture incompatible with giant garter snake occurrence. Thus, habitat restoration efforts in many parts of the former range of giant garter snakes will likely be ineffective without accompanying translocation.

Incorporating historic conditions into the analyses of contemporary species distributions provides valuable insight into factors limiting distribution and abundance in modified habitats and provides valuable information for resource managers. We suspect that the effects of historic habitat conditions on species distributions is a general phenomenon applicable to other poorly dispersing species persisting in highly modified landscapes and habitats. Effective conservation of species inhabiting altered landscapes will require not only looking forward to future challenges, but also looking backward to examine the ecological limitations operating on these species.

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