Habitat Suitability and Conservation of the Giant Gartersnake (*Thamnophis gigas*) in the Sacramento Valley of California

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Resource managers often have little information regarding the habitat requirements and distribution of rare species. Factor analysis-based habitat suitability models describe the ecological niche of a species and identify locations where these conditions occur on the landscape using existing occurrence data. We used factor analyses to assess the suitability of habitats for *Thamnophis gigas* (Giant Gartersnake), a rare, threatened species endemic to the Central Valley of California, USA, and to map the locations of habitat suitable for *T. gigas* in the Sacramento Valley. Factor analyses indicated that the niche of *T. gigas* is composed of sites near rice agriculture with low stream densities. Sites with high canal densities and near wetlands also appeared suitable, but results for these variables were sensitive to potential sampling bias. In the Sacramento Valley, suitable habitats occur primarily in the central portion of the valley floor. Based upon the results of the factor analyses, recovery planning for *T. gigas* will require an on-the-ground assessment of the current distribution and abundance of *T. gigas*, maintaining the few remaining natural wetlands and the practice of rice agriculture in the Sacramento Valley, and studying the effects of agricultural practices and land use changes on populations of *T. gigas*.

WILDLIFE conservation requires identifying the source of population declines and ameliorating threats to species. Often, little is known about the distribution or habitat requirements of rare species, which makes selection of conservation efforts difficult. Habitat suitability models (Guisan and Zimmermann, 2000) are particularly useful in these cases because these models can determine the habitat requirements of species and predict their locations on the landscape with limited data. Habitat suitability models can also be used to examine how habitat changes will likely affect a species. They define the habitat requirements of species or communities and can predict the distributions of species (Guisan and Zimmermann, 2000). Habitat suitability models also can be used to guide the selection of sites for the establishment of reserves and identify locations that might be suitable for repatriation or assisted colonization (Hoegh-Guldberg et al., 2008).

Two broad categories of habitat suitability models exist: those that require presence–absence data, and those that only require presence data (Hirzel et al., 2002). Approaches that require presence–absence data, such as occupancy modeling (MacKenzie et al., 2002), are generally more accurate (Brotons et al., 2004), provided they account for imperfect detection of individuals (MacKenzie et al., 2002). Certain situations, however, are more amenable to approaches such as factor analysis (Hirzel et al., 2002; Calenge and Basille, 2008) that require presence-only data. For example, expanding populations that have not yet occupied all suitable habitat, or declining species which have been extirpated from otherwise suitable habitat, result in absences unrelated to habitat suitability. In these circumstances, presence-only habitat suitability modeling outperforms methods based upon presence–absence data (Hirzel et al., 2001; Pearce and Boyce, 2006).

The Central Valley of California, USA, has experienced extensive anthropogenic habitat alteration in the last 150 years. The Central Valley has a Mediterranean climate, with hot, dry summers and mild, wet winters (Sivakumar et al., 2006). Historically, winter rains and snowmelt from the Sierra Nevada Mountains to the east resulted in the overflow of river channels and vast expanses of emergent wetland habitat throughout much of the Central Valley (Singer et al., 2008). In the late 19th and early 20th Centuries, construction of dams and conversion of land to agricultural uses resulted in an altered water regime and loss of most natural wetland habitat in the region (Frayer et al., 1989; James and Singer, 2008).

Reduction of the extent of wetland habitats in the Central Valley from 1.6 million ha in the 1850s to 200,000 ha in the mid-1980s (a loss of 86%; Frayer et al., 1989) resulted in the decline of many species dependent on wetland habitats, including *Thamnophis gigas* (the Giant Gartersnake). *Thamnophis gigas* is a large (to 1.6 m total length) semi-aquatic snake endemic to the Central Valley (Fitch, 1940; Hansen and Brode, 1980; Fig. 1), and has been state- and federally-listed as threatened because of habitat loss (California Department of Fish and Game Commission, 1971; U.S. Fish and Wildlife Service, 1993). The magnitude and extent of landscape and hydrologic alteration of the Central Valley is likely to have extirpated populations of *T. gigas* in areas that currently contain otherwise suitable habitat. We therefore used presence-only factor analyses, which perform better than presence–absence analyses when not all suitable habitat is occupied, to examine the niche of *T. gigas* and map the current suitability of habitat in the Sacramento Valley (northern portion of the Central Valley) for this rare snake. We use the map derived from our analyses to determine the extent of remaining suitable habitat in the Sacramento Valley, and direct future survey and conservation efforts for *T. gigas*. We also generalize the results of our factor analyses to assess potential threats to *T. gigas* in a changing climate and landscape.

MATERIALS AND METHODS

We sampled *T. gigas* at 26 sites throughout the Sacramento Valley from 1996 through 2005 using visual searches, floating aquatic funnel traps (Casazza et al., 2000), and incidental captures. Sampled sites were not uniformly distributed, but were located at project-specific sites determined by interest to funding agencies and permission for

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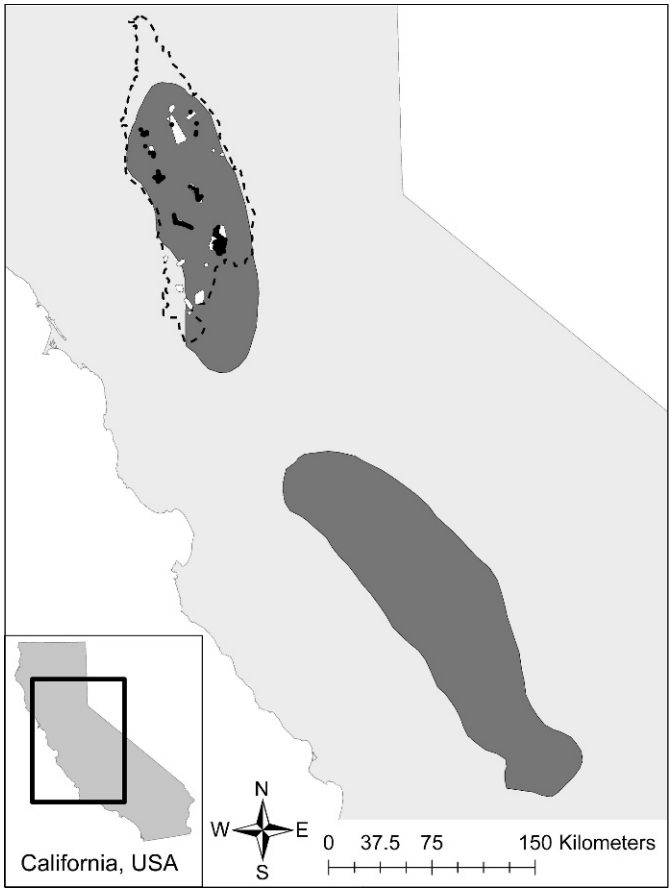

Fig. 1. The approximate historic range (re-drawn from Rossman et al., 1996) of *Thamnophis gigas* (dark gray), the location of the Sacramento Valley (dotted line), the locations of sites sampled from 1996 through 2005 (white polygons), and the locations of individual *T. gigas* (black dots).

access. Sites were nonetheless dispersed throughout the Sacramento Valley (Fig. 1), and many sites were selected without *a priori* knowledge of the occurrence of populations of *T. gigas*. Captured individuals (n = 1924) were measured, sexed, and given individual marks as part of a series of mark–recapture studies. We recorded the location of each capture with Global Positioning System (GPS), and used only the location of the initial observation of each individual in our analysis to avoid pseudoreplication.

To identify landscape-level variables important for the occurrence of *T. gigas*, we employed two complementary factor analyses (Calenge and Basille, 2008). We chose this analytical framework instead of occupancy modeling (MacKenzie et al., 2002) because *T. gigas* likely occupies only a portion of currently available suitable habitat (Hirzel et al., 2001; Pearce and Boyce, 2006). We also chose factor analyses instead of other presence-only techniques (Elith et al., 2006) because of their statistical basis and interpretability as different aspects of the relationship of occurrence of *T. gigas* to habitat conditions (Calenge and Basille, 2008). We used two complementary analyses, Ecological Niche Factor Analysis (ENFA) and Mahalanobis Distances Factor Analysis (MADIFA), to explore the relationship between the niche of *T. gigas* and the availability of habitats in the Sacramento Valley (Hirzel et al., 2002; Basille et al., 2008; Calenge et al., 2008). We also evaluated Mahalanobis distances as an alternative to MADIFA for mapping habitat suitability.

Habitat data for ENFA and MADIFA were derived from several raster maps. These maps included data on land use in the Sacramento Valley from Ducks Unlimited, the location and type of waterways from the National Hydrography Dataset (http://nhd.usgs.gov), and data on canopy and impervious cover from the National LandCover Dataset (http://landcover.usgs.gov; Table 1; Fig. 2). Maps were derived from data collected in the late 1990s and early 2000s at approximately the same time as our sampling. We selected variables for inclusion in the analysis using biological intuition and knowledge of the landscape of the Sacramento Valley. We included a variety of aquatic habitat types in our analyses (Table 1) to define the niche of this semi-aquatic snake. We differentiated rice agriculture from other agriculture because rice is the only crop inundated during the active season of *T. gigas* and might therefore provide habitat. In contrast, other agriculture in the Sacramento Valley consists primarily of vegetable crops, alfalfa, and fruit and nut orchards, which we expected would not provide habitat for *T. gigas*. Percent impervious cover was chosen because of its high correlation with human population density and anthropogenic structures, particularly roads. Percent canopy cover was selected to determine if occurrence of *T. gigas* was affected by tree density and shading. The native cell size in each raster was approximately 30 m × 30 m. We used density and percent cover variables from the native raster at 30 m × 30 m resolution, then resized cells to 300 m × 300 m by taking the mean value of cells within a 300 m × 300 m neighborhood in ArcMAP 9.2 (ESRI, 2006). This cell size was selected because it approximates the mean core activity area of individuals inhabiting hydrologically dynamic habitats (G. Wylie, unpubl. data) and because of computation limitations associated with calculating suitability of smaller cells at this regional extent. We used distance metrics for

Table 1. Comparison of Environmental Variables Used in the Ecological-Niche Factor Analysis (ENFA), Mahalanobis Distances Factor Analysis (MADIFA), and Mahalanobis Distances Habitat Suitability Map: Availability in the Sacramento Valley, Availability at Sampled Locations, and Usage by *Thamnophis gigas* (Calibration and Validation). All data are expressed as median (range).

Variable	Sacramento Valley	Sampled locations	*T. gigas* calibration	*T. gigas* validation
Canopy cover (%)	0.7 (0–92)	0.1 (0–38)	0.4 (0–33)	0.6 (0–27)
Impervious cover (%)	0.3 (0–84)	0.3 (0–36)	0.3 (0–36)	0.9 (0–54)
Distance to open water (m)	4,743 (0–26,298)	4,014 (0–14,904)	2,970 (0–9,070)	4,800 (0–11,420)
Distance to wetlands (m)	1,825 (0–29,149)	1,237 (0–8,469)	1,082 (0–5,692)	1,616 (0–6,462)
Distance to rice (m)	2,830 (0–57,126)	849 (0–36,522)	671 (0–3,912)	424 (0–24,770)
Distance to agriculture (m)	600 (0–22,997)	671 (0–3,613)	900 (0–3,612)	600 (0–3,759)
River or stream density (m/ha)	57 (0–468)	0 (0–272)	0 (0–193)	0 (0–311)
Canal density (m/ha)	36 (0–521)	189 (0–473)	199 (0–392)	175 (0–425)

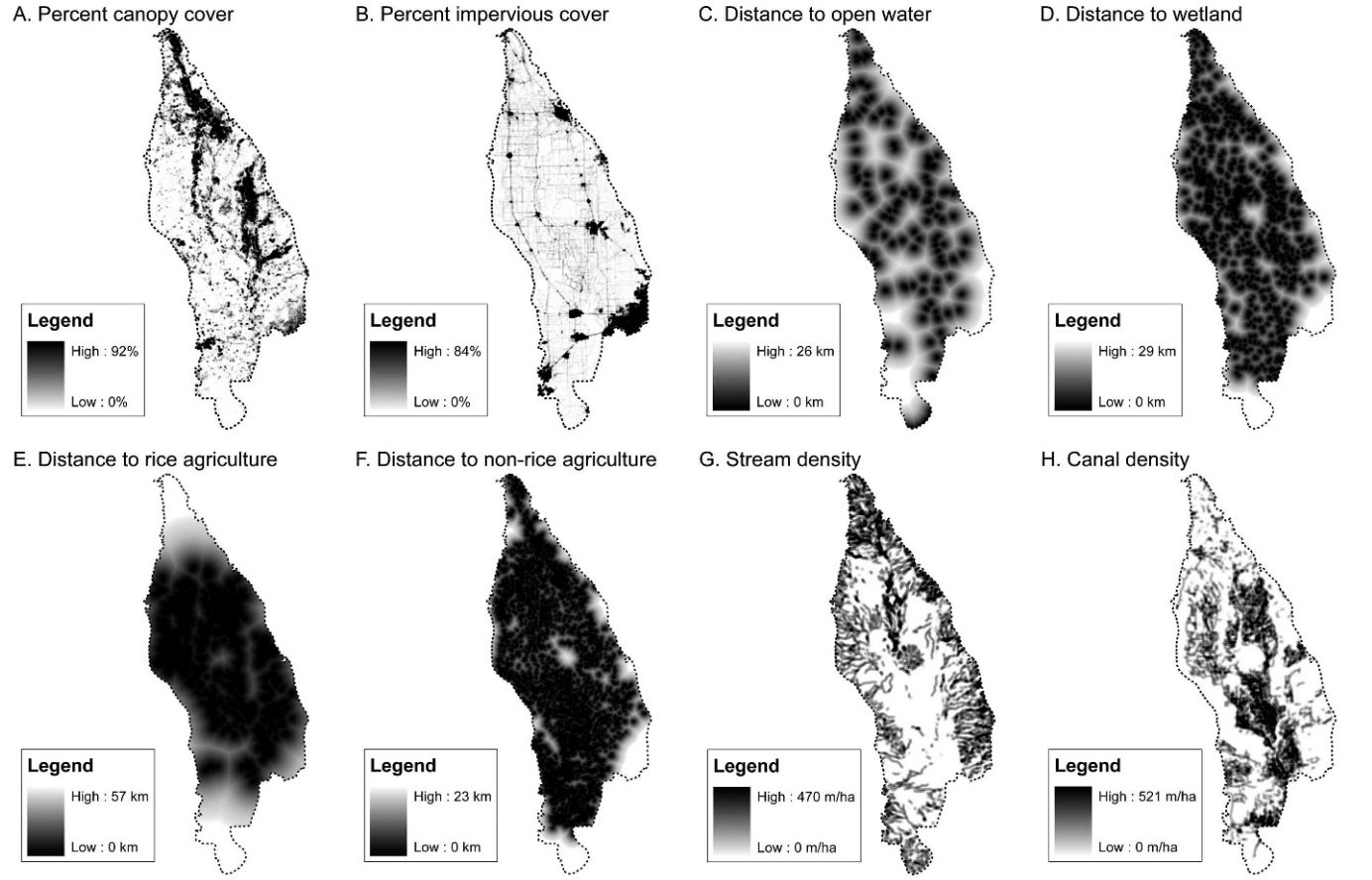

Fig. 2. Input maps used to examine the niche of *Thamnophis gigas* in the Sacramento Valley of California.

several variables to characterize suitability of the surrounding landscape while avoiding very large numbers of zeros and improving the central tendency of the data distributions. Because of the sensitivity of distance data to very small habitat patches, we generalized the land use raster to make the minimum habitat patch size 1 ha. We then calculated distances on a raster with 30 m × 30 m cells, then resized cells to 300 m × 300 m as for the density and percent cover variables. To make their distributions more symmetric and improve the performance of the factor analyses (Basille et al., 2008), all variables were log-transformed after the addition of a constant to avoid taking logs of zeros (percent canopy cover, percent impervious cover, river density, and canal density; constant = 0.1) and to reduce distortion caused by many very small and a few very large values (distance to wetlands, distance to open water, distance to rice agriculture, and distance to non-rice agriculture; constant = 100).

After construction of raster maps, we conducted ENFA, MADIFA, and Mahalanobis distances analyses using the package adehabitat (Calenge, 2006) in R 2.6.2 (R Development Core Team, 2008). For all analyses, we performed a principal component analysis (PCA) on the habitat variables, which eliminates collinearity and standardizes components to have a mean of zero and variance of one. We assessed presence of *T. gigas* in each raster cell (n = 307 cells with records out of 125,665 available cells), rather than using the count of individuals captured in each cell, to avoid problems associated with unequal sampling effort across sites. From these data, the ENFA extracts a marginality axis and multiple specialization axes (Hirzel et al., 2002; Calenge and Basille, 2008). Marginality describes the greatest multivariate distance between the niche and the available environment, and specialization describes how narrow the niche is relative to the remaining variation in the available environment. We determined how many specialization axes to retain based upon the presence of a large decrease in sequentially extracted eigenvalues. To determine which variables best explained the location and specificity of the niche of *T. gigas*, we calculated the correlation of each input variable with the marginality and extracted specialization axes. To assess the potential impact of sampling bias, we also conducted the ENFA using only sampled cells (n = 696) as the available environment. We tested the significance of this latter ENFA by randomly allocating the number of raster cells known to be occupied (n = 307) among all sampled raster cells (n = 696) 1000 times, and comparing the observed dominant eigenvalue to the dominant eigenvalues from the ENFA analyses for all random distributions of ''snake'' locations (Raes and ter Steege, 2007).

The MADIFA, in contrast to the ENFA, locates the directions in ecological space for which the niche is narrowest relative to the available environment (Calenge et al., 2008). As for the ENFA, we examined a barplot of the eigenvalues for a large decrease to determine how many axes to interpret, and examined the correlation of each input variable with the retained axes. We examined the goodness-of-fit (GOF) of the MADIFA by calculating the area between the empirical cumulative density of Mahalanobis distances derived from the first axis of the MADIFA for plots containing *T. gigas* and the empirical cumulative density for all plots in the Sacramento Valley, and dividing it by the

total area above the empirical cumulative density for all plots in the Sacramento Valley (Calenge et al., 2008). This represents how well the first axis of the MADIFA distinguishes the niche from the available environment relative to perfect discrimination, where all observed locations have a Mahalanobis distance of zero. To validate our MADIFA model and determine its predictive ability, we repeated the GOF procedure using snake location data collected from 2006–2009 at sites not included in the calibration dataset and independent records of *T. gigas* in the California Natural Diversity Database (CNDDB; California Natural Diversity Database, 2008) observed after 1990 (n = 121 raster cells with confirmed presence of *T. gigas*). As for the ENFA, we also conducted the MADIFA using sampled sites of the calibration data set to assess sensitivity of our results to sampling bias.

As a complement to the descriptions provided by ENFA and MADIFA, we used squared Mahalanobis distances to generate a habitat suitability map for *T. gigas* in the Sacramento Valley. Mahalanobis distances are the multivariate distances between the mean of the niche of the species and the habitat components at each mapped location (Calenge et al., 2008). We used this analysis to map the suitability of habitats for *T. gigas* because it uses all available information for constructing the habitat suitability map, whereas the MADIFA only uses the dominant extracted axis (or axes). Maps generated using Mahalanobis distances assume that smaller distances, which are most similar to the mean habitat requirements of the species, represent areas more likely to be occupied by the species (Calenge et al., 2008). Although the Mahalanobis distances can be biased if optimal habitat is not surveyed (Calenge et al., 2008), our sampling encompassed a range of habitats at study sites spread throughout the region that contains the vast majority of extant populations of *T. gigas*. Little habitat outside the Sacramento Valley is currently occupied by *T. gigas*; therefore, it is unlikely that highly suitable sites outside the sampled area but within the mapped region would have Mahalanobis distances much larger than expected. Because the Mahalanobis distances analysis we employed can be sensitive to correlated environmental variables (which can result in a singular variance-covariance matrix), we performed the Mahalanobis distances analysis on components extracted by the PCA. We calculated GOF for the Mahalanobis distances as for the first axis of the MADIFA, and validated the Mahalanobis distances model with the same data used for validation of the MADIFA.

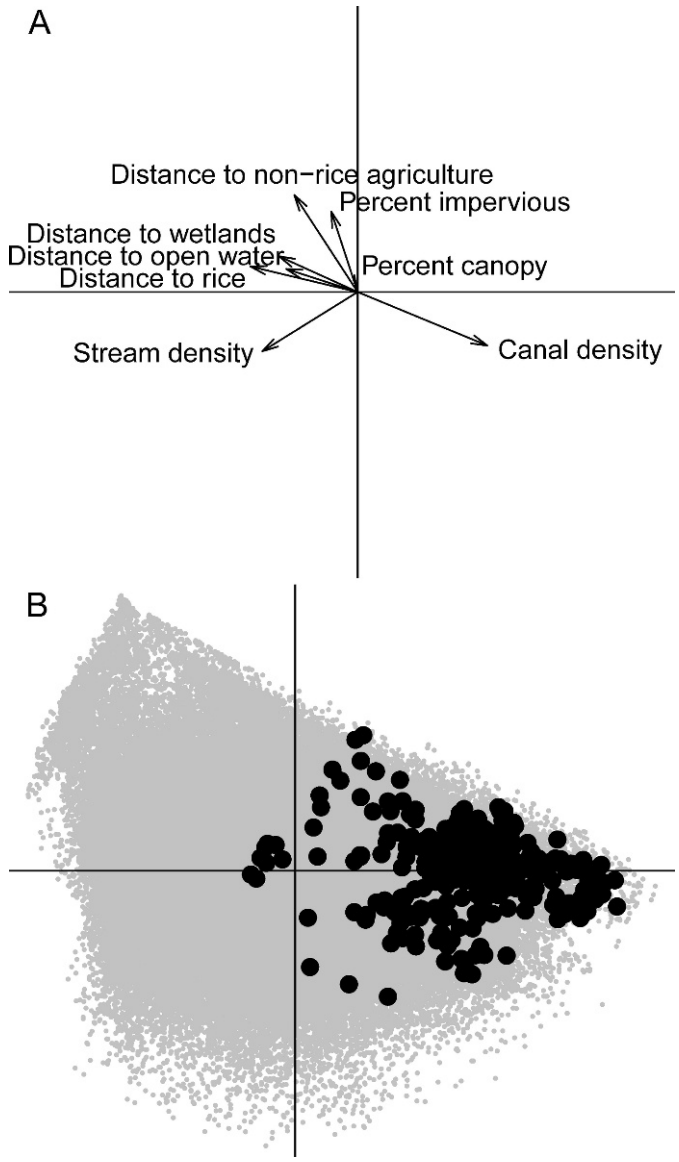

Fig. 3. Results of the Ecological-Niche Factor Analysis (ENFA) for *Thamnophis gigas* in the Sacramento Valley of California. (A) Graph of the correlation of the environmental variables with the marginality (x-axis) and first specialization (y-axis) axes from the ENFA; (B) factorial map of the niche of *T. gigas* on the marginality and first specialization axes of the ENFA. The light gray points in (B) indicate the available environment in the Sacramento Valley, and the black points indicate locations at which *T. gigas* occurred.

RESULTS

Characteristics of locations of *T. gigas* were different from the environment generally available in the Sacramento Valley, but were similar to sampled locations (Table 1). The randomization test indicated that the habitats used by *T. gigas* differed from sampled habitats (minimum simulated dominant eigenvalue = 1.10, maximum = 1.65, observed value = 2.16). The Sacramento Valley ENFA indicated that *T. gigas* occurred in areas with a dense network of canals (correlation with marginality axis: R = 0.69), close to rice agriculture (R = −0.40), with a low density of streams (R = −0.37), and close to open water (R = −0.36) and wetlands (R = −0.28) relative to available environments in the Sacramento Valley (Fig. 3A, 3B). Similarly, the sampled locations ENFA indicated that *T. gigas* occurred in areas close to rice agriculture (R = −0.53), with a low density of streams (R = −0.52), close to open water (R = −0.47), far from agriculture (R = 0.37), and with a high density of canals (R = 0.27). No clear break in eigenvalues for the description of the specialization of the niche of *T. gigas* was evident with either definition of availability.

The first axis of the MADIFA explained 46% of the differences in Mahalanobis distances between the niche of *T. gigas* and the Sacramento Valley, but the second axis only explained 14%. We therefore only interpreted the first axis of the MADIFA. The MADIFA indicated that the niche of *T. gigas* was narrowest relative to the available environment with respect to distance to rice agriculture (correlation with axis 1: R = −0.75), canal density (R = 0.74), stream density (R = −0.64), and distance to wetlands (R = −0.54). The first axis of the MADIFA predicted only 14% of its cases correctly

(as compared to perfect discrimination), and could not distinguish between validation locations of *T. gigas* and available habitats.

The results of the MADIFA for sampled sites only were similar to those of the Sacramento Valley MADIFA. The first axis of the sample MADIFA explained 36% of the differences in Mahalanobis distances between the niche of *T. gigas* and sampled sites. This axis of the sample MADIFA indicated that the niche of *T. gigas* was narrowest relative to sampled sites with respect to distance to rice ($R = -0.81$), stream density ($R = -0.56$), distance to agriculture ($R = 0.44$), distance to open water ($R = -0.42$), distance to wetlands ($R = -0.29$), and canal density ($R = 0.26$).

Because of the poor predictive performance of the MADIFA, we generated a habitat map based upon the squared Mahalanobis distances between the mean of the niche of *T. gigas* and available habitats in the Sacramento Valley. The Mahalanobis distances performed much better than the first axis of the MADIFA, predicting 67% of its cases correctly, and predicted independent locations 71% as well as it fit the data used in its construction. This corresponds to 99% of the locations of *T. gigas* in the calibration dataset and 83% of the locations of *T. gigas* in the validation dataset occurring in the top 50% of pixels in the Sacramento Valley as measured by squared Mahalanobis distance. The habitat suitability map constructed using squared Mahalanobis distances indicated that the central portion of the Sacramento Valley floor is most suitable for *T. gigas* (Fig. 4).

DISCUSSION

The results of the ENFA and MADIFA were in agreement on the major variables important for describing the habitat relationships of *T. gigas* in the Sacramento Valley. Both analyses indicated that *T. gigas* primarily occurs where a dense network of canals exists among rice agriculture and wetlands. The agreement of the marginality axis from the ENFA and the first axis of the MADIFA indicates that *T. gigas* occupies a narrow range of canal densities and distances to rice agriculture and wetlands at one end of the gradient of available environments in the Sacramento Valley. The presence of *T. gigas* was also negatively related to stream density. Therefore, *T. gigas* inhabits stagnant or slow-moving waterbodies with abundant emergent vegetation. The association of *T. gigas* with rice agriculture and canals is likely because these agricultural habitats have replaced nearly all natural wetlands in the Central Valley (Frayer et al., 1989), and are the only suitable habitats available in much of the Sacramento Valley.

The location of suitable habitats for *T. gigas* in the Sacramento Valley is primarily within rice growing regions on the floor of the valley. Because many populations are likely dependent upon rice agriculture and its supporting network of canals on private property that has not been surveyed, an important application of our habitat suitability map is to direct future survey efforts to determine the current distribution of the species. Our validation of the habitat suitability map allows us to tentatively estimate that 83% of occurrences of *T. gigas* will be in the top 50% of suitable pixels of the Sacramento Valley. This estimate requires validation using occupancy studies, and might be biased low if much suitable habitat is unoccupied. Furthermore, although the habitat suitability map predicts occurrences, it provides no information about the abundance of occupied sites unless one makes the inferential leap to assume a relationship between the likelihood of occurrence and abundance. Much of the most suitable habitat to the north and south of the Sutter Buttes (indicated by the light circle in the center of Fig. 4) remains unsurveyed, but has great potential to contain populations of *T. gigas*. Because these locations contain large areas of suitable habitat, they are potentially good sites for acquisition of land and establishment of reserves. Whether repatriation is a more appropriate conservation strategy will depend upon the results of future surveys. Repatriation might be a particularly important conservation tool in the San Joaquin Valley (southern portion of the Central Valley, containing the southern part of the species range in Fig. 1) where *T. gigas* has been largely extirpated, but restored wetlands provide suitable habitat. The primary utility of exploratory habitat suitability maps is to direct conservation efforts and future research, rather than to serve as definitive distributional maps.

The strong association of *T. gigas* with aquatic agricultural habitats has several conservation implications. The presence of water on the landscape, particularly during the active season (March–October) of *T. gigas*, is essential for the species to persist. Areas within the species' range, but without emergent aquatic habitats such as rice agriculture, canals, and wetlands, are unlikely to be inhabited by *T. gigas*. The dependence of many populations of *T. gigas* upon agricultural wetlands exposes them to habitat loss caused by changing agricultural practices, habitat degradation caused by canal and levee maintenance procedures, and contamination with agrochemicals (Santos et al., 1999). Where it inhabits rice fields, the diet (Santos et al., 2000), body condition (Santos and Llorente, 2004), and reproductive ecology (Santos et al., 2005) of *Natrix maura* (Viperine Snake), a European species ecologically similar to *T. gigas*, are strongly affected by agricultural practices, particularly the timing of flooding rice fields. At the community level, agricultural land use resulted in decreased biodiversity of reptiles in Catalonia (Ribeiro et al., 2009). Population density and body condition of *T. gigas* is greater in natural wetlands than rice-dominated landscapes (Wylie et al., 2010), but without rice agriculture, very few populations would remain extant. Regardless of whether rice agriculture has an overall positive or negative effect on *T. gigas* relative to historic habitat conditions, effective conservation of this species in the Sacramento Valley will require studies of the effects of agricultural practices on *T. gigas* and development of best management practices to ameliorate potential threats.

In addition to agricultural practices, *T. gigas* will likely be adversely affected by climate change. Climate change models predict that the climate of California's Sierra Nevada Mountains will become drier (Hayhoe et al., 2004; Barnett et al., 2008), potentially shrinking the area of habitats suitable for *T. gigas* through drying of wetlands and cessation of rice agriculture as the cost of water increases. Exacerbating the effects of climate change, the anthropogenic demand for water in the San Joaquin Valley and urbanized areas in southern California is likely to increase (Groves et al., 2005). As water demand increases, the revenue available to farmers from water transfers also increases, and farmers will be more likely to shift from water-intensive crops such as rice to crops that do not require inundation or to fallowing rice fields (Hooker and Alexander, 1998). Because many current populations of *T. gigas* are dependent upon rice as a source

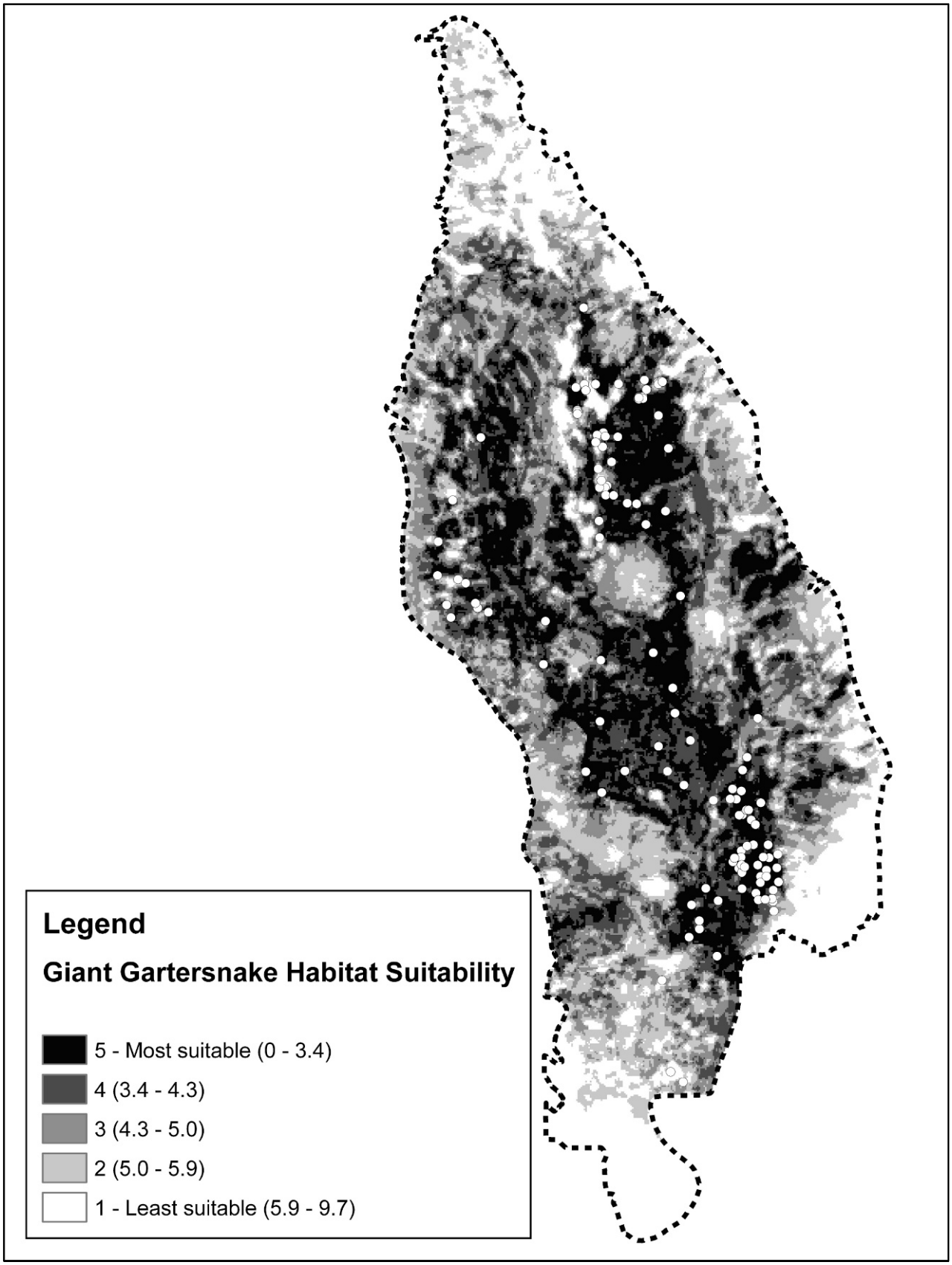

Fig. 4. Habitat suitability map for *Thamnophis gigas* in the Sacramento Valley based upon squared Mahalanobis distances. White dots indicate locations of *T. gigas* captures used for validation of the Mahalanobis distances model. The dashed line indicates the boundary of the Sacramento Valley. Numbers in parenthesis indicate the range of $\sqrt{(\text{Mahalanobis distance})^2}$ in each mapped category.

of emergent aquatic habitat in the fields themselves and in the irrigation canals providing water and drainage to the fields, transfer of water from rice agriculture to other uses will likely have detrimental effects on *T. gigas* and other wetland-dependent species in the Sacramento Valley (Elphick, 2000). Studies assessing the effects of water transfer practices on *T. gigas* are necessary to give farmers and resource protection agencies the tools they need to meet the challenges of decreased supply and increased demand for water in California.

The strong association of *T. gigas* with marsh and marsh-like (rice fields and canals) habitats is likely caused by several ecological traits. The diet of *T. gigas* consists of larval and adult amphibians and small fish (Rossman et al., 1996). Marshes, canals, and flooded rice fields all contain these prey in abundance during most of the active season of *T. gigas* (G. Wylie, unpubl. data). Even if streams and ponds or lakes contain abundant prey, the structure of shallow water emergent habitats might improve the foraging efficiency of *T. gigas* (Mullin and Mushinsky, 1995; Mullin et al., 1998). In addition to providing foraging habitat, the structure of emergent aquatic habitats likely provides *T. gigas* with additional benefits. The hot, dry climate of the Sacramento Valley during the active season of *T. gigas* likely exceeds the critical thermal maximum of this species routinely on summer afternoons. Although many aquatic habitats could provide thermal refuge, fast-moving or deep water habitats are likely well below the field-preferred body temperature (29.8°C; Wylie et al., 2009) of *T. gigas*. Relatively stable and warm water temperatures in shallow wetlands might also allow nocturnal activity where it would not otherwise be possible (Hansen, 1980). Therefore, thermoregulatory conditions might restrict the niche of *T. gigas* to slow-moving, shallow, emergent aquatic habitats. In addition to thermoregulation, the emergent vegetation that characterizes the habitat of *T. gigas* likely provides more visual cover from predators, such as raptors and otters, than open water habitats. Predator avoidance might be particularly important for *T. gigas*, because predation has been suggested as an important mechanism for the evolution of both extreme wariness and large size in this species (Hansen, 1980). Future research should be directed at a mechanistic understanding of the distributional limits of *T. gigas*.

Our sensitivity analysis revealed several important patterns with respect to the results of both the ENFA and MADIFA. In particular, using both the Sacramento Valley and sampled sites as available habitat resulted in defining the niche of *T. gigas* to consist of sites near rice agriculture with a low density of streams. In contrast to the close agreement for rice and streams, defining available habitat as sampled sites resulted in decreased importance of wetlands and canals for describing the niche of *T. gigas*. In addition to these differences, analysis of sampled sites also indicated a negative effect of non-rice agriculture, a feature that was not evident in the analysis of the Sacramento Valley. These results suggest that our sampling frame was biased toward sites close to wetlands and non-rice agriculture, and with high canal densities. The bias toward wetlands was not unexpected, because contracts often involved surveying public lands restored to wetlands from agriculture. The reduced importance of wetlands when examined by sampled sites, however, is likely because many of these wetlands have not yet been colonized. Therefore, although the relationship of *T. gigas* with wetlands and canals was positive in most analyses, elucidating the strength of the association of *T. gigas* with these habitats will require sampling sites more representative of the Sacramento Valley as a whole. We can confidently conclude, however, that *T. gigas* is associated with rice agriculture and areas with low stream densities in the Sacramento Valley. The strength of the negative association of non-rice agriculture with the niche of *T. gigas* in the Sacramento Valley merits further study.

Despite their agreement on major variables associated with the occurrence of *T. gigas*, the ENFA and MADIFA exhibited some differences. For example, the ENFA did not exhibit any dominant specialization axes. This can occur if much of the information on specialization is explained in the same variables as marginality or if the restriction of the niche has a complex relationship with the environmental variables. We suggest that the former is the case because of the similarity of dominant variables extracted by the ENFA and MADIFA. Although the ENFA identified the habitat of *T. gigas* closer to open water than generally available in the Sacramento Valley, MADIFA indicated that the range of distances to open water at which *T. gigas* occurred was not particularly narrow. This pattern was likely because rice agriculture, canals, and wetlands are generally found close to or contain areas of open water. Therefore, although *T. gigas* is found relatively close to open water relative to the Sacramento Valley, the range of distances to open water was not particularly narrow. This pattern would not have been identifiable with the use of a single method of habitat suitability modeling.

Although the MADIFA was useful for describing the narrowness of the niche, the dominant axis of the MADIFA had poor predictive capabilities and was therefore ill-suited for mapping habitat suitability. The Mahalanobis distances, however, performed much better for distinguishing the habitat of *T. gigas* from the Sacramento Valley as a whole. This was likely because the Mahalanobis distances used all information in the habitat variables to map habitat suitability, but the MADIFA used only a single extracted component that contained less than 50% of the information available in the habitat data. MADIFA was originally developed to describe the narrowness of the niche and generalize habitat maps using fewer variables than a Mahalanobis distances analysis. For *T. gigas*, however, the generalization implicit in the MADIFA resulted in poor discriminant ability between occupied and available habitats. The Mahalanobis distances analysis did not suffer this difficulty; however, it did little to clarify the habitat relationships of *T. gigas*. We therefore view different approaches to analysis and mapping of suitable habitat as complementary.

Relatively few broad geographic studies of habitat suitability for snake species exist. Two studies on the Iberian Peninsula used ENFA to examine the niche and habitat suitability of snakes. In contrast to *T. gigas*, the niche of the viperid *Vipera latastei* (Lataste's Viper) differed relatively little from the range of environmental conditions on the Iberian Peninsula, and its niche was correspondingly broad (Santos et al., 2006). The distribution of *V. latastei* is therefore likely limited by human modification of the landscape, but competition with congeners may also contribute to its limited occurrence (Santos et al., 2006). The colubrid *Coronella austriaca* (Smooth Snake), however, was restricted to sites characterized by steep slopes with relatively high amounts of dry season precipitation (Santos et al., 2009). Because it is found in relatively extreme

environments, climate change is expected to negatively impact *C. austriaca* at the southern limits of its range (Santos et al., 2009). In addition to studies of habitat suitability using ENFA, species-distribution modeling was used to determine that the invasion of rainforest habitat by three African savanna snake species because of deforestation would potentially be offset by climate change (Freedman et al., 2009). Characterization of hibernacula at the northern limits of the range of *Pantherophis alleghaniensis* (=*Elaphe obsoleta*, Eastern Ratsnake) using PCA followed by ANOVA indicated that hibernacula were not located at random, but also that many suitable sites were not used as hibernacula (Prior and Weatherhead, 1996). Despite these studies, patterns in habitat suitability and the impacts of land-use changes across snake species remain unresolved.

Habitat suitability modeling is a valuable exercise to support the conservation of species about which little is known. It can inform conservation by defining the habitat relationships of species and identifying locations at which a species is likely to occur. These locations can be used to direct future survey effort, and identify sites suitable for establishment of reserves or repatriation of extirpated populations. Many options exist for mapping habitat suitability from presence-only data, and we recommend that researchers use multiple approaches to identify different aspects of the niche of species and to map the location of suitable habitats on the landscape. Potential biases induced by the sampling frame should also be examined by conducting analyses on sampled sites and comparing these to analyses using the entire study area. Regardless of the techniques used, however, it is vitally important to determine the goodness-of-fit of the models and validate them with independent data to ensure the reliability of inference.

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