Herpetological Conservation and Biology 10(2):633–644.
Submitted: 17 December 2014; Accepted: 5 August 2015; Published: 31 August 2015.

TERRESTRIAL ECOLOGY OF SEMI-AQUATIC GIANT GARTERSNAKES (*THAMNOPHIS GIGAS*)

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***Abstract.*—Wetlands are a vital component of habitat for semiaquatic herpetofauna, but for most species adjacent terrestrial habitats are also essential. We examined the use of terrestrial environments by Giant Gartersnakes (*Thamnophis gigas*) to provide behavioral information relevant to conservation of this state and federally listed threatened species. We used radio telemetry data collected 1995–2011 from adults at several sites throughout the Sacramento Valley, California, USA, to examine Giant Gartersnake use of the terrestrial environment. We found Giant Gartersnakes in terrestrial environments more than half the time during the summer, with the use of terrestrial habitats increasing to nearly 100% during brumation. While in terrestrial habitats, we found Giant Gartersnakes underground more than half the time in the early afternoon during summer, and the probability of being underground increased to nearly 100% of the time at all hours during brumation. Extreme temperatures also increased the probability that we would find Giant Gartersnakes underground. Under most conditions, we found Giant Gartersnakes to be within 10 m of water at 95% of observations. For females during brumation and individuals that we found underground, however, the average individual had a 10% probability of being located > 20 m from water. Individual variation in each of the response variables was extensive; therefore, predicting the behavior of an individual was fraught with uncertainty. Nonetheless, our estimates provide resource managers with valuable information about the importance of protecting and carefully managing terrestrial habitats for conserving a rare semiaquatic snake.**

Key Words.—California; Central Valley; core terrestrial habitat; garter snake; radio telemetry; wetland buffer

INTRODUCTION

Wetlands are a major and obvious component of habitat for amphibians and semiaquatic reptiles. Many amphibians are entirely dependent upon wetlands for breeding, and semiaquatic reptiles, including many turtles and some snakes, conduct most of their activity within wetlands. Adjacent terrestrial habitats, however, are also critical for all but a handful of fully aquatic species. Indeed, a large body of literature has accumulated in the past two decades calling attention to the terrestrial component of habitat for amphibians (Semlitsch 1998; Trenham 2001; Semlitsch and Bodie 2003; Regosin et al. 2005; Dodd and Cade 2008), turtles (Burke and Gibbons 1995), and semiaquatic snakes (Roe et al. 2003). A major conclusion of studies of the use of terrestrial habitat by amphibians is that legislation designed to maintain or improve water quality is inadequate to protect the core habitat requirements of most semiaquatic herpetofauna in the United States (Burke and Gibbons 1995; Semlitsch 1998; Semlitsch and Bodie 2003; Roe et al. 2004; Crawford and Semlitsch 2007). Furthermore, landscape characteristics at larger spatial scales can affect the persistence and presence of herpetofauna at individual wetlands and regional scales through metapopulation processes (Gibbons 2003; Roe et al. 2004; Roe and Georges 2007; Harper et al. 2008; Ficetola et al. 2009).

Although consensus exists that terrestrial areas adjacent to wetlands comprise essential core habitat for herpetofauna, how different species use upland habitats varies. Therefore, the need for species-specific information remains. Terrestrial habitat composition affects species in different ways (Fellers and Kleeman 2007; Dodd and Cade 2008), and species vary in both their vagility and ability to persist in terrestrial landscapes (Roe et al. 2003; Porej et al. 2004; Roe and Georges 2007; Ficetola et al. 2009). Thus, a species-specific approach to defining core terrestrial habitats of semiaquatic herpetofauna is necessary (Fellers and Kleeman 2007), particularly for species of conservation concern.

Giant Gartersnakes (*Thamnophis gigas*; Fig. 1) comprise a species of semi-aquatic snake precinctive to marshes of the Central Valley of California. Largely because of the loss of > 93% of wetlands in the Central Valley (Frayer et al. 1989; Garone 2007), Giant Gartersnakes are listed as Threatened by the State of California (California Department of Fish and Game Commission 1971) and the United States (U.S. Fish and Wildlife Service 1993). Despite their aquatic habits, Giant Gartersnakes overwinter in terrestrial habitats

FIGURE 1. An adult Giant Gartersnake, *Thamnophis gigas* (Photographed by Matt Meshriy, US Geological Survey).

(Hansen 1986) and also spend much of their active season in terrestrial refuges near water (USGS, unpubl. data). Little information exists regarding the use of terrestrial habitats by Giant Gartersnakes. This information is vital for Giant Gartersnake conservation because many agricultural and other land management activities, including canal and levee maintenance, disturb ground in the vicinity of wetlands. It is unknown to what extent these activities might result in direct mortality of Giant Gartersnakes or destruction or degradation of their habitat.

The objective of our study was to describe the terrestrial ecology of semi-aquatic Giant Gartersnakes. In particular, we were interested in the probability that Giant Gartersnakes will occur in the terrestrial environment, and the probability that they are underground while in the terrestrial environment. We further examined the probability of Giant Gartersnakes occurring in the terrestrial environment as a function of distance from water. In each of these cases, we examined how time (both day of year and time of day), temperature, and individual characteristics affected use of the terrestrial environment. The results of our study provide important information about the terrestrial behavior of Giant Gartersnakes for resource managers.

MATERIALS AND METHODS

Study sites.—We conducted our study at six sites in the Sacramento Valley (northern portion of the Central Valley), California, and one site at the eastern edge of the Sacramento-San Joaquin Delta between 1995 and 2011 (Table 1). The Badger Creek wetlands are a series of naturally occurring marshes at the eastern edge of the Sacramento-San Joaquin Delta. The Colusa Drain is a regional drainage canal in the western Sacramento Valley that is bordered by a levee and rice fields. Colusa National Wildlife Refuge (NWR) is managed for multiple species, and consists of seasonal (flooded in winter) and permanent wetlands, uplands, and irrigation ditches in the western Sacramento Valley. Gilsizer Slough, in the eastern Sacramento Valley, is a remnant drainage feature of the Yuba River that is now surrounded by farmland (mostly rice agriculture). Restoration activities converted approximately 150 ha of row crops to marshes at Gilsizer Slough in the early 2000s. At the time of our study, the Natomas Basin (in the southeastern Sacramento Valley) largely consisted of rice agriculture and its associated infrastructure of canals. The Road Z site, in the north-central Sacramento Valley, consisted of a series of canals in a matrix of rice agriculture. The Sacramento NWR is managed for multiple species, and consists of seasonal (flooded in winter) and permanent wetlands, uplands, and irrigation ditches in the northwestern Sacramento Valley.

Field methods.—At each study site, we captured individual Giant Gartersnakes by hand and in modified floating minnow traps (Casazza et al. 2000). We retained individuals > 180 g for intracoelomic implantation of a radio transmitter (Model SI-2T, mass = 9 or 11 g, Holohil Systems Ltd., Carp, Ontario, Canada) by certified veterinarians at the University of California, Davis or the Sacramento Zoo following standard procedures (Reinert and Cundall 1982). We allowed individuals to recover 1–2 weeks in the laboratory. In addition to surgical implantation of radio transmitters, we taped transmitters (Model R1620, mass = 1.3 g, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) to individuals in the field to study the feasibility of using externally attached transmitters in 2003, 2004, 2006, and 2009 (Wylie et al. 2011). Regardless of whether they were surgically implanted or attached externally, transmitters were < 5% of the mass of each individual. We released individuals at their location of capture, and located them 5–7 d per week during the active season (April–September) and once or twice per week during brumation. Time of observations varied, but we conducted nearly all radio telemetry during daylight hours. We used portable receivers (Model R4000, Advanced Telemetry Systems, Inc., Isanti,

TABLE 1. Number of male and female Giant Gartersnakes (*Thamnophis gigas*) tracked at each site in the Sacramento Valley, California, and the years in which snakes at each site were monitored. The abbreviation NWR = National Wildlife Refuge.

Site	Females	Males	Unknown	Years monitored
Badger Creek	11	1	1	1996–1998
Colusa Drain	30	7	0	2004, 2006–2007
Colusa NWR	75	31	4	1996–1998, 2000–2004
Gilsizer Slough	61	23	0	1995–1997, 2007–2011
Road Z	1	0	0	2008–2009
Natomas	13	0	0	1998–1999, 2003
Sacramento NWR	1	0	0	1997
Total	192	62	5	1995–2004, 2006–2011

Minnesota, USA) and three-element Yagi antennas (Arrow Antenna, Cheyenne, Wyoming, USA) to locate individuals, and attempted to visually observe each individual whenever possible. At each location, we recorded the location of the individual (Universal Transverse Mercator, North American Datum 1927) with a handheld GPS (< 7 m accuracy; eTrex or GPS 12, Garmin International, Inc., Olathe, Kansas, USA). We recorded behavior, air, substrate, and water temperatures, and habitat data, including whether the snake was in a terrestrial environment. We also recorded whether it was visible aboveground, the substrate on which it occurred, and its visually estimated distance from water in six categories (0, < 1, 1–3, 3–10, 10–20, and > 20 m).

Analytic methods.—We used hierarchical logistic regression to examine patterns in the probability that Giant Gartersnakes used the terrestrial environment, and the probability that terrestrial locations would be of snakes underground or under vegetation. We examined differences in these probabilities based upon individual sex and size, and several observation-specific measures. We used a quadratic function of Julian date as a continuous predictor to examine seasonal patterns, a quadratic function of time of day to examine circadian patterns, and a quadratic function of temperature to examine thermal effects on Giant Gartersnake use of the terrestrial environment. We also allowed terrestrial behavior of the sexes to differ seasonally by including an interaction of sex with the quadratic effect of date. For the analysis of the probability of being underground or under vegetation, we also included an interaction of the quadratic effects of date and time, which allowed circadian patterns in aboveground activity to vary seasonally. We also included a logit-normal random intercept for individual to account for different numbers of observations and different baseline probabilities of use of the terrestrial environment among individuals.

To examine the probability that Giant Gartersnakes would occur in the terrestrial environment as a function of distance from water, we conducted two complementary analyses. In the first analysis, we used a hierarchical ordinal logistic model to examine the probability that Giant Gartersnakes occurred in the binned distance classes. We examined the effects of individual sex and size on the distribution of distances from water, and also examined the effects of several observation-specific measures. We included an effect of whether the individual was observed on the surface or underground to examine whether the distance from water changed with surface activity. We used a quadratic function of Julian date as a continuous predictor to examine seasonal patterns, a quadratic function of time of day to examine circadian patterns, and a quadratic function of temperature to examine thermal effects on Giant Gartersnake distances from water. We also allowed the terrestrial distribution of the sexes to differ seasonally by including an interaction of sex with the quadratic effect of date. In addition to the effects of these variables and their interactions, we also included a logit-normal random intercept for individual to account for different numbers of observations and different baseline probabilities of use of the terrestrial environment among individuals.

Because the last bin in the categorical field data included all values > 20 m, we used a continuous model of distance from water based upon the coordinates of each individual location. This allowed estimation of the probability distribution for distances of Giant Gartersnakes > 20 m from water. After eliminating locations of snakes that were in water (based upon the substrate recorded in the field), we calculated the Euclidean distance from each snake location to the nearest mapped feature in the USGS National Hydrography Dataset (http://viewer.nationalmap.gov/viewer/nhd.html? p=nhd) using the Near tool in ArcGIS 10.1 (ESRI, Redlands, California, USA). We then analyzed the distribution of distances using three different potential models: an exponential distribution, a gamma distribution, and a log-normal distribution. We used the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002) to choose among these models. For the best-fit model, we then added the same predictor variables as for the categorical field data, including the individual random intercept.

For all analyses, we evaluated the support for effects of covariates using indicator variables on model

TABLE 2. Posterior model probabilities for terrestrial behavior of adult Giant Gartersnakes (*Thamnophis gigas*) at seven sites in the Sacramento Valley, California, 1995–2011. A "1" indicates that the variable was included in the model; a "0" indicates that the variable was omitted from the model. Models are listed in order of decreasing probability. Only models with a posterior probability > 0.001 are shown. The superscript 2 is a variable squared. NA indicates variables not included in the model set.

	Explanatory Variable											
Response Variable	Date	Date^2	Time	Time^2	Date^2 × Time^2	Temp	Temp.^{2}	Sex	Length	Sex × Date^2	Under-ground	Posterior Probability
Probability in Terrestrial Environment	1	1	1	0	NA	0	0	1	0	1	NA	0.965
	1	1	1	0	NA	1	0	1	0	1	NA	0.015
	1	1	1	0	NA	0	0	1	1	1	NA	0.010
	1	1	0	0	NA	1	0	1	0	1	NA	0.009
	1	1	1	1	NA	0	0	1	0	1	NA	0.002
Probability underground	1	1	1	1	1	1	1	0	0	0	NA	0.956
	1	1	1	1	1	1	1	0	1	0	NA	0.017
	1	1	1	1	1	1	0	0	0	0	NA	0.015
	1	1	1	1	1	1	1	1	0	0	NA	0.012
Categorical distance from water	1	1	0	0	NA	1	1	1	0	1	1	0.951
	1	1	0	0	NA	1	1	1	1	1	1	0.048
GIS-based distance from water	1	0	0	0	NA	0	0	0	0	0	1	0.961
	1	1	0	0	NA	0	0	0	0	1	1	0.016
	1	1	0	0	NA	0	0	0	0	0	1	0.016
	1	0	0	0	NA	0	0	1	0	0	1	0.005

coefficients (Kuo and Mallick 1998; Royle and Dorazio 2008). All parameters were given vague priors (log-normal intercepts and coefficients = N[mean = 0, variance = 100]; log-normal standard deviation [SD] of random effects = U[min = 0, max = 100]; logit-scale intercepts and coefficients = N[0,10]; logit-scale SD of random effects = U[0,10]; and indicator variables = Bern[0.5]). We analyzed all models using five chains of 20,000 iterations each after a burn-in of 20,000 iterations, and thinned the output by a factor of 10 so that inference was based upon 10,000 samples from the stationary posterior distribution. We examined history plots for each parameter for evidence of lack of convergence, and found none. For all parameters, we represented posterior distributions with the median and 95% credible interval (0.025 quantile–0.975 quantile). We also calculated posterior predictive intervals, as these represent the confidence limits for how an unknown individual would use the terrestrial environment under specified conditions. All analyses were conducted by running JAGS (JAGS version 3.4.0. Available from http://sourceforge.net/projects/mcmc-jags/files/ [accessed 21 October 2014]) from R (R version 3.1.0. Available from http://cran.us.r-project.org/ [accessed 21 October 2014]) using the package rjags (rjags version 3-13. Available from http://cran.r-project.org/web/packages/rjags/index.html [Accessed 21 October 2014]).

RESULTS

We obtained 27,218 observations of 259 individuals at seven sites over 16 y (Table 1). The sample of females was much larger than that of males, and females accounted for 89% of observations. The probability that Giant Gartersnakes were found in terrestrial habitats varied with season, time of day, sex, and an interaction of sex with season (Table 2). Giant Gartersnakes were more likely to be in terrestrial locations during the inactive season than during the summer, with males exhibiting less seasonal variation than females (Fig. 2). In mid-July, when Giant Gartersnakes were least likely to be in terrestrial environments, females had a probability of 0.59 (0.53–0.66) of being in a terrestrial environment, and males had a probability of 0.68 (0.57–0.77) of being in a terrestrial environment (Fig. 2). The odds of Giant Gartersnakes being in terrestrial locations was higher earlier in the day than later in the day (e.g., the odds of being in a terrestrial environment were 1.11 [1.07–1.15] times greater at 1210 than at 1445; Fig. 3). Much individual variation existed in the probability of being in a terrestrial environment (logit-normal SD for individual-specific random intercept = 1.67 [1.49–1.88]). Despite relatively high precision in estimates of the average probability of a Giant Gartersnake occurring in a terrestrial environment, predicting whether a given

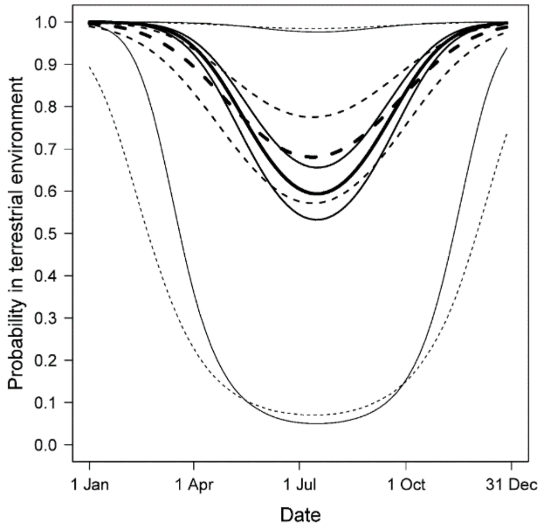

FIGURE 2. Probability of use of the terrestrial environment by female (solid lines) and male (dashed lines) Giant Gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 1995–2011, throughout the year. Bold lines indicate posterior medians, medium-weight lines indicate 95% posterior credible intervals, and light lines indicate 95% posterior predictive intervals.

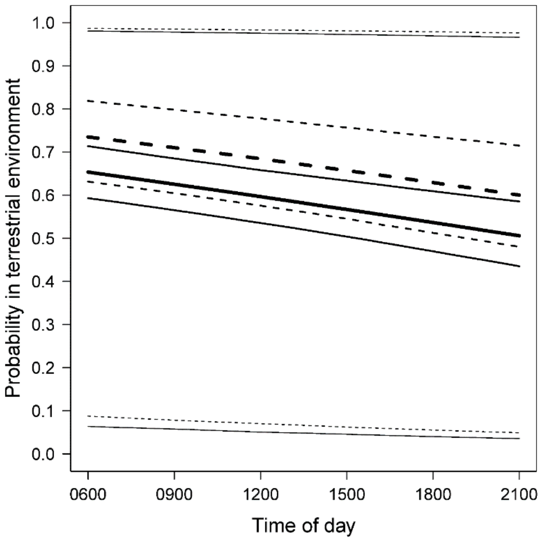

FIGURE 3. Probability of use of the terrestrial environment by female (solid lines) and male (dashed lines) Giant Gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 1995–2011, based upon time of day. Values presented for early July. Bold lines indicate posterior medians, medium-weight lines indicate 95% posterior credible intervals, and light lines indicate 95% posterior predictive intervals.

individual would be in a terrestrial environment was accompanied with great uncertainty (Figs. 2 and 3). For example, on a given day during the summer, a randomly selected individual has anywhere between a 5% and 97% probability of being in the terrestrial environment (Fig 2.). Similarly, it is nearly impossible to predict whether a randomly selected individual would be in the terrestrial environment at a given time of day (Fig. 3).

When in terrestrial habitats, the probability that Giant Gartersnakes were found in subterranean refuges or under other cover varied with quadratic effects of season, time of day, and temperature, including an interaction of quadratic effects of season and time of day (Table 2). The use of subterranean refuges did not vary with individual snake characteristics. Giant Gartersnakes were likely to be in terrestrial refuges at all times of day during the inactive season, and were least likely to be in terrestrial refuges in the early afternoon during the early summer (Fig. 4). The lowest probability of the average Giant Gartersnake in a terrestrial setting being underground (0.60 [0.53–0.67]) occurred in the early afternoon (approximately 1430) in late June (Fig. 4). Giant Gartersnakes were also more likely to be underground at extreme temperatures (Fig. 5), with the lowest probability of being underground when in terrestrial environments occurring at an ambient air temperature of 23 °C (probability of being underground at this temperature = 0.64 [0.58–0.70]; Fig. 5). As for the probability of being in a terrestrial environment, much individual variation existed in the probability of being underground (logit-normal SD for individual-specific random intercept = 1.85 [1.63–2.12]). Predicting whether a given individual will be on the surface or underground is therefore fraught with uncertainty, despite high posterior precision of estimates of the behavior of an average Giant Gartersnake (Figs. 4 and 5).

The best-fit model of the field-collected distance-to-water categories indicated that season interacting with sex, a quadratic function of temperature, and position relative to the surface affected the distance from water at which Giant Gartersnakes were found (Table 2). The distance from water at which males were found was consistent among seasons, but females were farther from water in the winter and closer to water in summer (Fig. 6). In summer, 96% (95–97%) of the locations of the average female Giant Gartersnake were < 10 m from water. In winter, however, only 74% (66–80%) of locations of the average female Giant Gartersnake were within 10 m of water (Fig. 6). Males exhibited much less seasonal variation, with approximately 96% (93–98%) of locations of the average male Giant Gartersnake occurring within 10 m of water in all seasons (Fig. 6). Giant Gartersnakes were also closest to water when ambient air temperatures were highest (at 40 °C, 93% [91–95%] of locations of the average Giant Gartersnake were within 3 m of water; at 20 °C, 88% [84–91%] of locations of the average Giant Gartersnake were within 3 m of water; Fig. 7). Snakes also tended to be at greater distances from water when they were underground than when they were observed on the surface (Fig. 7). The average individual observed on the surface was within 10 m of water for 96% (95–97%) of observations, but

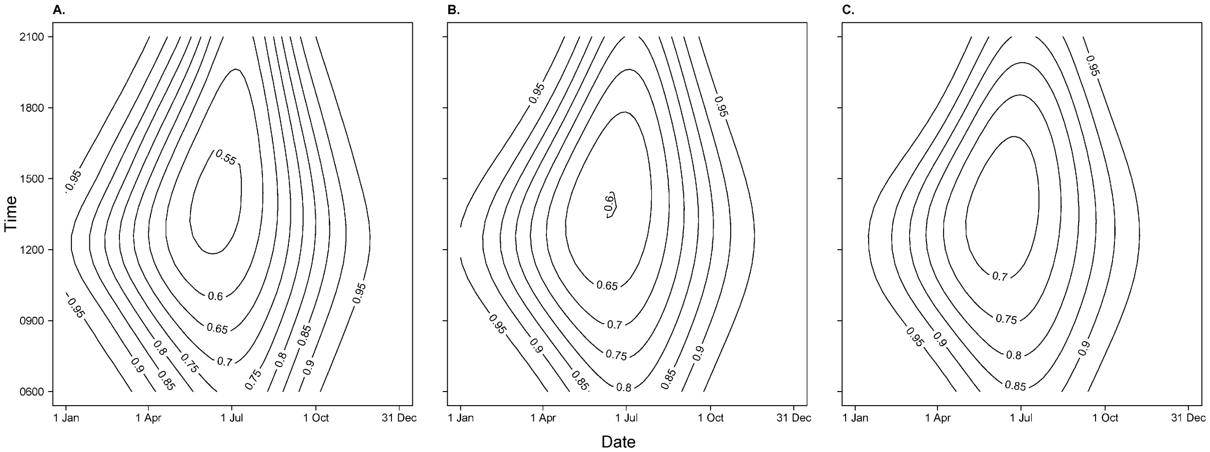

FIGURE 4. Probability of Giant Gartersnakes (*Thamnophis gigas*) being hidden underground or under vegetation, given that they were in a terrestrial environment, in the Sacramento Valley, California, 1995–2011, throughout the year by time of day. A). Posterior 0.025 quantile, B). Posterior median, and C). Posterior 0.975 quantile of the mean probability of being hidden underground or under vegetation.

only 83% (78–87%) of locations of the average individual observed underground were < 10 m from water. Individuals varied greatly in the distances at which they were observed from water (SD of logit-normal random effect = 1.95 [1.76–2.15]). Therefore, predicting the distance at which an individual would be found from water is difficult. The most precise prediction based upon the model results is that at ambient air temperatures of 40 °C, 73% of Giant Gartersnake locations would be < 20 m from water.

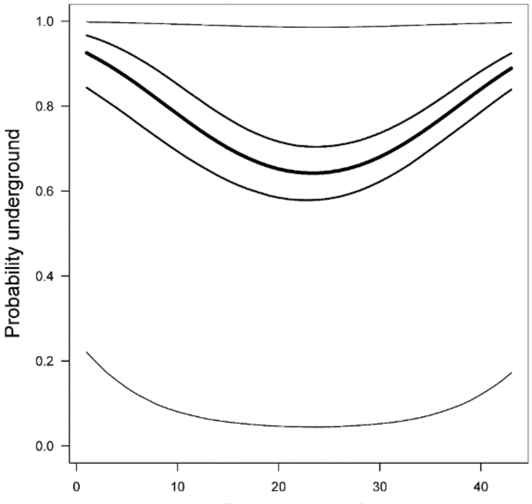

FIGURE 5. Probability of Giant Gartersnakes (*Thamnophis gigas*) being hidden underground or under vegetation, given that they were in a terrestrial environment, in the Sacramento Valley, California, 1995–2011, based upon air temperature (shaded bulb 1 m above ground). Bold lines indicate posterior medians, medium-weight lines indicate 95% posterior credible intervals, and light lines indicate 95% posterior predictive intervals.

The best-fit model of GIS-based distance to water was a log-normal model (Table 3). Adding covariates to this base model indicated that date and snake position relative to the surface were the best predictors of distance to water (Table 2). The effect of date was very small, with 95% of locations of the average Giant Gartersnake on the surface occurring within 31 m (27–36 m) of water on 1 January, and the same proportion occurring within 25 m (22–29 m) of water on 1 December. The effect of snake position was also small, with 95% of locations of the average Giant Gartersnake on the surface occurring within 28 m (24–32 m) of water, and the same proportion of locations of the average Giant Gartersnake underground or other cover occurring within 24 m (21–27 m) of water (Fig. 8). Individual variation in the GIS-based distance to water was slightly less than for other response variables, but was still substantial (SD of log-normal individual random effect = 0.92 [0.84–1.02]). This resulted in a high degree of uncertainty when predicting distance of a random individual from water, with a random individual on the surface on 1 July having a 95% probability of occurring within 174 m of water; a random individual underground on the same date has a 95% probability of occurring within 148 m of water (Fig. 8).

DISCUSSION

Based upon our results, conservation of Giant Gartersnakes will require the protection of upland areas near wetlands in addition to wetlands themselves. Despite their semiaquatic habits, locations of the average Giant Gartersnake occurred in terrestrial habitats more than half of the time, and Giant Gartersnakes occurred almost exclusively in terrestrial habitats during winter.

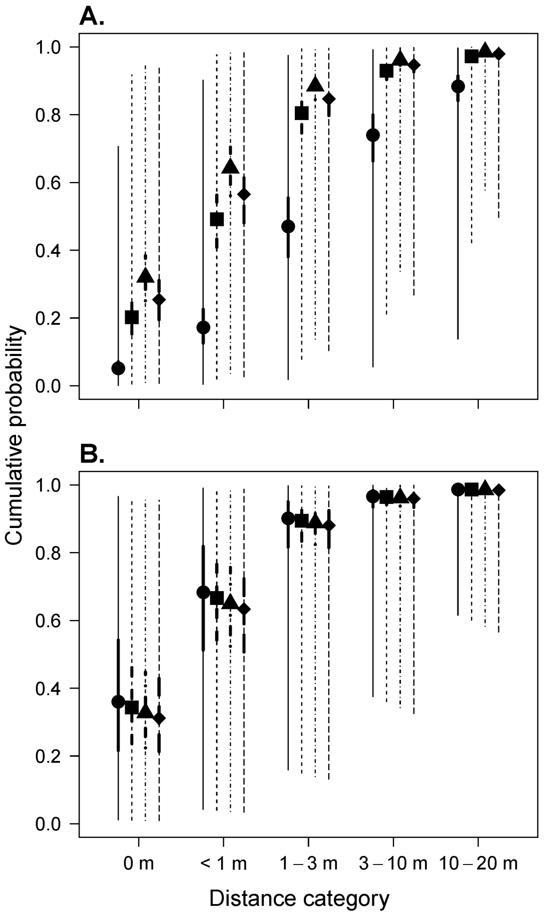

FIGURE 6. Cumulative probability of A. female, and B. male Giant Gartersnake (*Thamnophis gigas*) distances from water in winter (01 January, dots and solid lines), spring (01 April, squares and dotted lines); summer (01 July, triangles and dash-dot lines), and fall (01 October, diamonds and dashed lines), based upon distance categories collected in the field in the Sacramento Valley, California, 1995–2011. Bold lines represent 95% credible intervals; light lines represent 95% predictive intervals.

Although the average Giant Gartersnake occurs within 10 m of water 95% of the time in mid-summer, the average individual that is underground, or females during winter, exceed 20 m from water approximately 10% of the time. Furthermore, individual variation in all aspects of terrestrial ecology of Giant Gartersnakes was substantial, and based upon our models some individuals would likely be affected by activities in uplands up to 174 m from water. Limiting ground disturbance near wetlands is therefore critical for protecting habitat and avoiding mortality of individuals. Given the high probability of Giant Gartersnakes occurring in subterranean terrestrial refuges and at greater distances from water during brumation, ground-disturbing activities at this time could be especially detrimental to Giant Gartersnake populations.

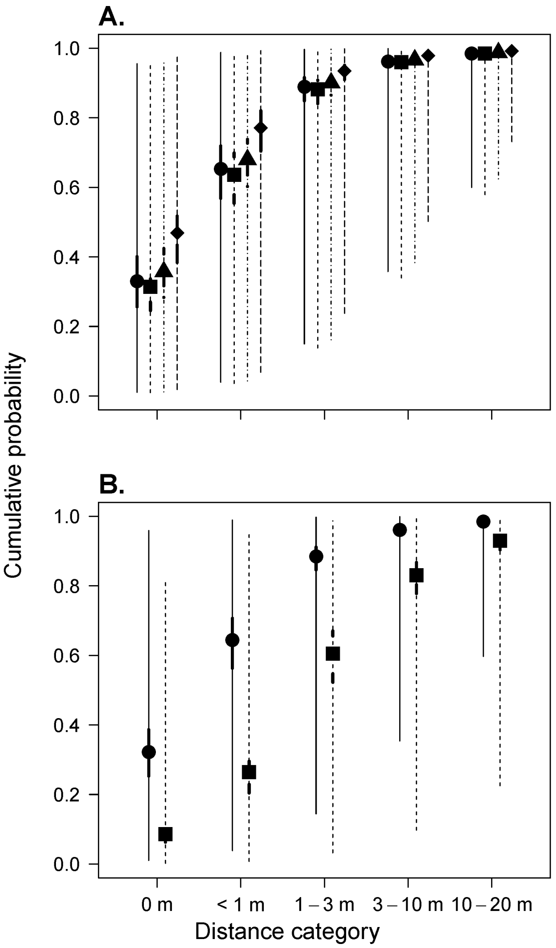

FIGURE 7. Cumulative probability of Giant Gartersnake (*Thamnophis gigas*) distances to water A). At 10 °C (dots and solid lines), 20 °C (squares and dotted lines), 30 °C (triangles and dash-dot lines), and 40 °C (diamonds and dashed lines) ambient air temperature, and B). When on the surface (dots and solid lines) and when underground (squares and dotted lines) based upon distance categories collected in the field in the Sacramento Valley, California, 1995–2011. Bold lines represent 95% credible intervals; light lines represent 95% predictive intervals.

Despite the importance of terrestrial habitats for Giant Gartersnakes, we recognize that ground-disturbing activities are necessary for maintaining much of what currently comprises Giant Gartersnake habitat in the Sacramento Valley: rice agriculture and its supporting infrastructure of canals. Even where marshes have been restored for Giant Gartersnakes, periodic maintenance activities often involve ground disturbance. Although disturbing or harming some individuals during earth-moving activities near marshes, canals, and rice fields is likely inevitable, careful excavation and attentive biological monitors can reduce mortality of unearthed snakes (Eric Hansen, pers. comm.). Minimizing earth-moving activities to the extent possible, and when they must occur, conducting them during early afternoons in summer, when snakes are most likely to be using aquatic habitat, would likely minimize negative effects to Giant Gartersnake populations. Furthermore, conducting earth-

TABLE 3. Model selection results for distributional models for GIS-based distances of Giant Gartersnakes (*Thamnophis gigas*) from water in the Sacramento Valley, California, 1995–2011. The abbreviation pD is the effective number of parameters. Models are listed in order of decreasing support.

Model	Mean deviance	pD	DIC	ΔDIC
Log-normal	81,790	2	81,790	0
Gamma	83,420	2	83,420	1,630
Exponential	84,473	1	84,480	2,690

moving activities over a small area within a single season would likely minimize the risk of extirpating Giant Gartersnake populations.

Terrestrial management activities not directly related to Giant Gartersnake management, such as vegetation removal (mowing, burning, dragging, or grubbing) and rodent abatement (particularly grouting or backfilling burrows), also have the potential to disturb or harm Giant Gartersnakes. Although vegetation management is necessary to prevent succession and reduce the encroachment of woody vegetation, which is detrimental to Giant Gartersnakes (USGS, unpubl. data), maintaining some herbaceous vegetative cover within core terrestrial habitats will likely reduce exposure of snakes to predators and environmental extremes during terrestrial movements. Mowing and burning will be least likely to negatively affect Giant Gartersnakes if these activities are conducted while Giant Gartersnakes have a high probability of being underground: during fall and winter, during mornings and evenings, and at extreme ambient temperatures (< 10 °C or > 35 °C). Ground-disturbing activities (e.g., dragging, grubbing, and grouting or backfilling burrows) within core terrestrial habitat are particularly insidious for Giant Gartersnakes because they can entomb snakes with no opportunity for observation or rescue. Therefore, minimizing their application in areas inhabited by Giant Gartersnakes would likely reduce snake entombment. In contrast to mowing and burning, soil-disturbing activities have the greatest potential for negative effects on Giant Gartersnakes when they occur when snakes are most likely to be underground. Future research on the selection and patterns of use of burrows by Giant Gartersnakes would be useful to further inform avoidance and minimization measures where soil disturbance near wetlands cannot be avoided.

Prohibitions against certain activities that might result in the Take (as defined by the Endangered Species Act) of Giant Gartersnakes include a work window that allows working in or near Giant Gartersnake habitat only between 1 May and 1 October. Our results suggest that this work window is likely to minimize risk to Giant Gartersnake populations. It must be recognized, however, that at least half of Giant Gartersnake activity, even during the active season, occurs in terrestrial environments, albeit very near wetlands. Our results indicate that caution is needed in these terrestrial habitats to avoid disturbance or harm to Giant Gartersnakes, regardless of the timing of work. Translocation of snakes to a new location outside the affected area might not be an effective tool to avoid Take of Giant Gartersnakes disturbed by earth-moving activities (Dodd and Seigel 1991, Reinert 1991; Reinert and Rupert 1999, Germano and Bishop 2009), and needs to be evaluated for its efficacy.

Although terrestrial habitats are essential for Giant Gartersnakes in the current landscape of the Sacramento Valley, it is unclear if this was true prior to the flood control and water storage projects of the 19th and 20th centuries. Historically, vast Tule (*Schoenoplectus acutus*) marshes and shallow lakes in the Central Valley of California (Frayer et al. 1989; Garone 2007) provided habitat for Giant Gartersnakes (Fitch 1940; Wright and Wright 1957). Occurrence in these expansive marshes suggests that Giant Gartersnake reliance on terrestrial habitats in the contemporary landscape might be caused by limitations of current habitats. Muskrat (*Ondatra zibethicus*) and North American Beaver (*Castor canadensis*) lodges, dense piles of Tule thatch, and other accumulations of vegetation likely provided structural attributes within historic marshes that are absent from many contemporary managed marshes and actively removed from water conveyances. We suspect that Giant Gartersnakes made use of this cover within historic marshes, and that the crayfish and mammal burrows in which Giant Gartersnakes are often found today are the closest proxy to the historic within-marsh refuges that the modern landscape has to offer.

Giant Gartersnakes are not unique in their requirement of both terrestrial and aquatic habitats. A large number of reptiles and amphibians require both habitats for different parts of their life cycles. Many amphibians breed and spend a larval period in streams or ponds, but have terrestrial habits as adults. The amount of core terrestrial habitat around breeding wetlands required by amphibians ranges from 27 m for stream-breeding salamanders (Crawford and Semlitsch 2007) to > 290 m for pond-breeding anurans and salamanders (Semlitsch 1998; Trenham 2001; Semlitsch and Bodie 2003; Regosin et al. 2005). All aquatic turtles lay their eggs on land; a study of multiple species in South Carolina indicated that a distance of 104 m from the wetland edge was required to encompass 90% of nests (Burke and Gibbons 1995), and a distance of 198 m was required

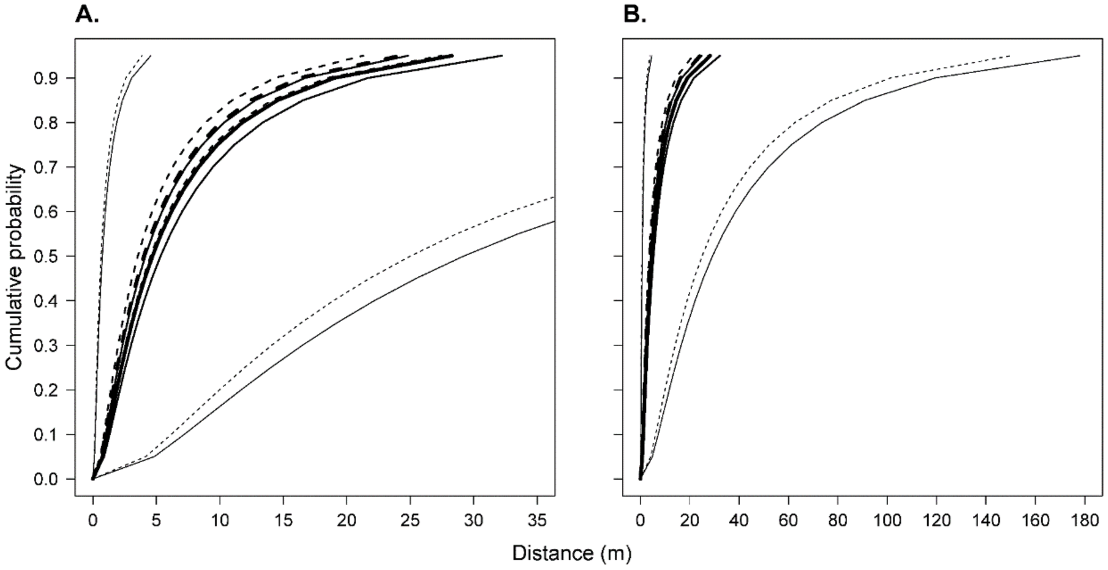

FIGURE 8. Cumulative probability of Giant Gartersnake (*Thamnophis gigas*) distances to water when on the surface (solid lines) and when underground (dashed lines) based upon GIS-based distances to water features in the Sacramento Valley, California, 1995–2011. Bold lines represent posterior medians, medium-weight lines represent 95% credible intervals, and light lines represent 95% posterior predictive intervals. A. and B. differ in scale on the x-axis to better represent credible and predictive intervals, respectively.

across 31 species in the United States and Canada to encompass the same proportion of nests (Steen et al. 2012). Core terrestrial habitat radii of up to 304 m (Semlitsch and Bodie 2003) have been recommended for semi-aquatic snakes, but the use of terrestrial habitats varies widely among species. For example, in northern Indiana and southern Michigan, Plain-bellied Watersnakes (*Nerodia erythrogaster*) traverse greater distances through terrestrial habitat and use more wetlands than sympatric Common Watersnakes (*N. sipedon*), which are much more closely tied to aquatic habitats (Roe et al. 2003, 2004). In particular, Plain-bellied Watersnakes were found in uplands in nearly 30% of observations, and were occasionally found > 100 m from wetlands (Roe et al. 2003). Giant Gartersnakes spent a greater proportion of time in terrestrial environments than Plain-bellied Watersnakes, and although the amount of core terrestrial habitat required by the average Giant Gartersnake is less than most of these other studies, accounting for individual heterogeneity in the use of terrestrial habitats results in core terrestrial habitat zones comparable to those of many of these other herpetofauna (e.g., 95% of locations of a random individual would occur within 174 m of water). Indeed, our posterior predictive limits represent the variation expected in empirical observations upon which most other studies of core terrestrial habitat are based. Furthermore, it must be recognized that maintaining connectivity among populations for viable metapopulation dynamics will require much greater terrestrial zones comprised of appropriate habitat for dispersal if aquatic connectivity is not maintained (Gibbons 2003; Porej et al. 2004; Roe and Georges 2007; Harper et al. 2008; Ficetola et al. 2009). Adequate connectivity of aquatic habitat via terrestrial dispersal could be particularly problematic for Giant Gartersnakes, which occur in a highly modified agricultural landscape (Halstead et al. 2014).

Results of the analyses based on categorical, field-estimated distance and continuous GIS-measured distance to water differed somewhat. In particular, the GIS-based distances resulted in a best-fit model with fewer parameters than the field collected data, and the estimated effects of date and position relative to the ground surface were smaller in the GIS-based analysis than the analysis based on field data. There are several potential causes for these differences. Given the relatively small distances from water of many Giant Gartersnake observations, GPS error might have been large enough to mask patterns in the data caused by predictor variables. In addition to GPS error, many small water features might not have been mapped, potentially biasing results based on GIS calculations. In general, we think that the distance data collected in the field are more reliable, and we prefer to base conclusions about the distance Giant Gartersnakes are found from water on data collected in the field. Because these data were limited to distances < 20 m, the GIS-based analysis is useful for inference about the distribution of Giant Gartersnakes at greater distances from wetlands, where GPS error and other potential confounding factors are less influential.

Although it has long been recognized that Giant Gartersnakes use terrestrial habitats, our study provides the first quantitative assessment of the extent to which these snakes rely on uplands. Our results suggest that active season use of terrestrial habitats is more extensive than previously assumed, but that the distance from which the average Giant Gartersnake is found from water is relatively small (within 30 m). Nonetheless, individual variation in the use of the terrestrial environment makes it difficult to predict whether an individual will be in a terrestrial environment, whether it will be underground, and how far it will be from water. Therefore, completely avoiding potential negative effects of terrestrial habitat disturbance to individual Giant Gartersnakes will be difficult. Although complete avoidance of disturbance to and mortality of Giant Gartersnakes associated with habitat management, flood control, and construction activities is infeasible, limiting such activities or modifying them to minimize ground disturbance near wetlands and canals will likely improve the health of Giant Gartersnake populations.

Conservation implications.—Several patterns evident in our results can assist with planning to minimize the potential for negative effects of terrestrial management activities to Giant Gartersnake populations. Giant Gartersnakes are most likely to be terrestrial in the fall, winter, and early spring, so avoiding ground-disturbing activities, especially those with the potential to entomb snakes, at these times would likely reduce negative effects on Giant Gartersnakes. Avoiding activities that can entomb snakes in the mornings, evenings, and overnight, and at temperatures below 15 °C or above 30 °C, when Giant Gartersnakes in terrestrial environments are likely to be underground, also would likely reduce negative effects on Giant Gartersnakes. In contrast, management activities like burning and mowing, which disturb surface vegetation but not the ground, might be better conducted when Giant Gartersnakes are more likely to be underground. Even with these precautions, ground-disturbing activities are likely to pose a danger to Giant Gartersnakes. Our results also indicate that activities closer to wetlands would affect a greater proportion of the local population. Limiting ground disturbance to relatively small stretches of canal or small sections of wetlands, and leaving intact terrestrial habitat with burrows and herbaceous vegetative cover adjacent to wetlands and canals near work areas, could help minimize the potential for ground disturbance to reduce the abundance of Giant Gartersnake populations.

*Acknowledgments.—*Funding for this research was provided by a number of agencies, including CalFed, the California Department of Water Resources, the Nature Conservancy, the U.S. Army Corps of Engineers, the U.S. Bureau of Reclamation, and the U.S. Fish and Wildlife Service. We thank the Nature Conservancy, U.S. Army Corps of Engineers, U.S. Fish and Wildlife Service, Wildlands, Inc., and private landowners for access to study sites. Cory Overton provided valuable comments that improved an earlier version of this manuscript. Pamela Gore and Lisa Parker provided administrative support. This work would not have been possible without the help of dozens of biological technicians. Snakes were handled in accordance with the University of California, Davis, Animal Care and Use Protocol 9699 and as stipulated in U.S. Fish and Wildlife Service Recovery Permit TE-020548-5. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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