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The spatial ecology of a species is a vital component of informed management and restoration plans, yet little is known about how animals use restored or constructed habitat. We assessed home ranges, core areas, and habitat selection of the federally threatened Giant Gartersnake (*Thamnophis gigas*) using rice agricultural habitat and recently constructed wetlands used as conservation banks. Space use patterns were estimated from radio tracking 19 unique adult female snakes over 2 years at a site that is the center of conservation efforts for the species. Home ranges (95% kernel density contour) and core areas (50% kernel density contour) were estimated for size, configuration, and overlap of the home range utilization distributions. Generalized linear mixed-effects models were used to assess habitat influences on microhabitat use. Contrary to expectations, but consistent across years, we found home ranges in the agricultural habitat were on average 80% smaller and had less variation among individuals than those in the constructed wetlands. Snakes in agricultural habitat also had greater and more uniform home range overlap as indicated by the utilization distribution overlap index. We combined all of the snakes to analyze microhabitat selection and used a matched location-random point design. Vegetation patch edges were used more often than interior locations in patches greater than six meters in diameter. This indicates that habitat complexity is an important consideration for habitat conservation plans. We were unable to detect differences in habitat use based upon vegetation composition at a small spatial scale. Temperature also influences reptile habitat selection, and a thermal description of the three macrohabitats (terrestrial vegetation, emergent vegetation, and open water) at our site showed extreme afternoon temperatures limit the use of terrestrial surface habitat by the Giant Gartersnake. The restricted home ranges observed in the snakes in agriculture suggest we need further investigation into dispersal movements and habitat connectivity to better inform regional conservation planning. Recovery efforts for the Giant Gartersnake, including construction and management of new wetlands, will benefit from greater knowledge of their space use patterns described by our research.

Giant Gartersnake Spatial Ecology in Agricultural and Constructed Wetlands

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of me thesis to any reader upon request.

Patricia M. Valcarcel, Author

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CONTRIBUTION OF AUTHORS

Drs. Rosenberg, Halstead, and Wylie were involved with the design of Chapter 2, and Drs. Rosenberg and Halstead also aided in the writing of Chapter 2.

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Chapter 1

INTRODUCTION

The Giant Gartersnake is a threatened species endemic to the Central Valley in California. It is a semi-aquatic species requiring upland habitat throughout the year and aquatic habitat during their active season because they feed exclusively on aquatic species. California has lost 91% of its original wetlands, and this loss of wetlands has been the primary reason for the decline of this species (USDI, 1994; USFWS, 2006). The distribution of Giant Gartersnakes has been restricted to areas within the Central Valley where rice, a wetland crop, is grown. Some believe rice fields offer suitable habitat because they provide flooded areas, emergent vegetation, and upland habitat bordering fields; rice fields are included in many habitat conservation plans (USFWS, 2006). However, Wylie et al. (2010) found that snakes in more disturbed areas had lower body condition than snakes in less disturbed, more natural areas. It is also unknown how agricultural habitat affects Giant Gartersnake movement.

Spatial ecology is a discipline that looks at patterns in the landscape with respect to ecological events, and is useful in understanding how animals move in relation to their environment. Concepts within this discipline, such as individual home range or habitat selection, can be applied to the Giant Gartersnake and serve as a foundation to informed management by improving prediction of species-level responses to changes in their environment. Using knowledge of a species' home range and habitat selection has become a common tool in conservation planning (Bingham and Noon, 1997; Kernohan et al., 2001; Ciofi et al., 2007), yet many factors influence the spatial ecology of a species. These factors include cover, population densities, food items, and individual-level processes (Rosenzweig, 1991; Tufto et al., 1996; Borger et al., 2006; Indermaur et al., 2009); therefore, it is important to have basic knowledge of the space-use of a species to direct future research efforts. These future efforts can focus on the mechanisms underpinning habitat selection important for making effective management decisions (Ripper et al., 2007).

Our goal in undertaking this research was to provide an understanding of the basic spatial ecology of the Giant Gartersnake in both agricultural wetlands (rice fields and surrounding drainages) and constructed wetlands built as part of conservation planning for the species. Our intention was to use both observational methods and experimental methods in this study. We used observational methods to describe general movement patterns of the Giant Gartersnake in the two habitat types and the thermal environment, which plays an important role in reptile habitat use (Reinert, 1993; Row and Blouin-Demers, 2006). We also used the thermal data along with hourly climate data from a nearby weather station to form a predictive model of temperature at the microhabitat level with which we planned to input in models to understand habitat selection. Lastly, we conducted an *in situ* experiment to explain a possible mechanism related to vegetative cover that may underlay these movement patterns. Chapter 2 is focused on the observational data and analysis and prepared as a manuscript to be submitted to a peer-reviewed journal. Chapter 3 briefly discusses the temperature model and experimental manipulation along with general conclusions.

CHAPTER 2

GIANT GARTERSNAKE SPATIAL ECOLOGY IN AGRICULTURAL AND CONSTRUCTED WETLANDS

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INTRODUCTION

Spatial ecology is the study of spatial patterns as they relate to ecological events, and when applied to species, it provides an important tool for management. Inherent in spatial ecology is the concept of home range. Home range reflects important aspects of an animal’s ecology, such as breeding grounds and food resources (Burt, 1943). Generally, home ranges are heterogeneous and encompass a variety of both macro- and microhabitats. Knowledge of how a species uses these habitats can tell us what resources may be important for conserving that species. Thus, spatial ecology with emphasis on individual home ranges and habitat use can help inform conservation efforts (Bingham and Noon, 1997), especially for species with complex life histories (Camper, 2009).

Landscape structure and resource distribution influence both home range size and shape (Ebersole, 1980; Tufto et al., 1996; Said and Servanty, 2005; Borger et al., 2006; Indermaur et al., 2009). Landscape fragmentation can influence home range by promoting or restricting movement. Response to fragmentation depends on many factors including fragment size and the connectivity and distance between fragments. Several hypotheses predict how fragmentation will affect individual home ranges, including fission (decrease in size and overlap between individuals), fusion (increase in overlap), and expansion (increase in size) (Ims et al., 1993; Andreassen et al., 1998; Verbeylen et al., 2009). Knowledge of how a species moves in response to changes in its habitat is critical in determining the focus of conservation efforts and predicting how individuals will react to those efforts.

California’s Central Valley has undergone extensive habitat modification and fragmentation because of agricultural practices (USDI, 1994). Restoration and conservation efforts in the Central Valley, especially for threatened and endangered species, will need to consider agricultural land use in order to succeed. A prime example is conservation planning for the threatened Giant Gartersnake (*Thamnophis gigas*), an obligate wetland species endemic to this area (USFWS, 1999). Currently, Giant Gartersnake distribution is largely restricted to the northern portion of the Central Valley where rice, a wetland crop, is dominant (Fig. 1). Giant Gartersnakes require flooded areas with emergent vegetation during the active season for feeding and cover and upland habitat for shedding, giving birth, and over-wintering. Rice farmland may meet a subset of this species’ habitat requirements, but the distribution of macro- and microhabitats of rice farmlands is very different from natural or constructed wetlands. We posit that these distribution differences in landscape structure will result in fundamental differences in Giant Gartersnake use of rice agriculture as compared to wetlands.

Constructed wetlands within the matrix of rice agriculture provide an excellent opportunity to compare Giant Gartersnake home ranges and habitat use between these structurally different habitat types. Agricultural habitat has high disturbance, pesticide and herbicide levels associated with farming practices, and drainage maintenance that entails dredging to remove silt and vegetation. Agricultural habitat may be more locally fragmented (fine-grained) than constructed wetlands because these maintenance procedures and farming practices create unevenly distributed aquatic vegetation patches with lengths of drainage without any vegetation. Wylie et al. (2010) also described lower body condition of Giant Gartersnakes in more disturbed areas when compared with less disturbed and more natural areas. For these reasons, we assumed agricultural habitat would be lower in quality than wetland habitat for Giant Gartersnakes. Under this assumption, we predicted an expansion response by snakes in agricultural areas that result in larger home ranges than snakes in constructed wetlands. The alternative is that snakes in agricultural habitat have smaller ranges because this habitat is either higher in quality or there is a higher degree of fragmentation (coarse-grained). If it is because of a high degree of fragmentation, we would expect a fusion response, and snakes in this habitat would exhibit restricted movements, increased overlap, and decreased variation in home range size (Tufto et al., 1996; Hinam and St. Clair, 2008; Verbeylen et al., 2009).

Home range response to landscape structure aids understanding of second-order selection (selection of individual home ranges within the landscape; Johnson, 1980), but it is also important to understand third-order selection, usage within the home range. Macro- and microhabitat distribution can affect within home range movement and use by individuals. For reptiles, thermoregulation greatly influences habitat use and movement (Huey et al., 1989; Reinert, 1993; Row and Blouin-Demers, 2006). Gravid female viviparous snakes are particularly selective of thermal microhabitats for proper embryonic development (Charland, 1995). The thermal quality of a habitat may be so low that it cannot be considered available habitat for snake use (Huey et al., 1989). We hypothesized that thermal quality of the three macrohabitats used by the Giant

Gartersnake in California’s Central Valley (terrestrial, emergent, and open water [without vegetation]) would influence the amount of functionally available habitat for the snake. Specifically, the afternoon temperatures make the surface of terrestrial macrohabitat too hot; therefore, unusable by the snake, and reduce the amount of available habitat.

As described above, selection is scale-dependent, and microhabitat characteristics such as the vegetation composition can also affect use by individuals. Composition of bare ground, litter, water, submergent vegetation, emergent vegetation, and terrestrial vegetation will likely influence habitat selection by the Giant Gartersnake. We also posited that rice will be used differently than non-rice emergent vegetation because of possible differences in prey abundance, timing of rice growth, and structure of rice fields. We hypothesized that an increase in non-rice emergent vegetation and water would increase use by Giant Gartersnakes because of thermal quality and foraging opportunities during the active season.

Vegetation structure is also an important aspect of microhabitat use. It is possible that dense patches of emergent vegetation may decrease sunlight and hinder snake movement and prey abundance. Cultivated rice is grown in a way that produces a dense vegetation patch and unmaintained wetlands can also form large patches of tules (*Schoenoplectus* spp.), cattails (*Typha* spp.), and a non-native primrose (*Ludwigia peploides*). In northern temperate climates, many snake species select habitat edges more often than they are proportionally available (Blouin-Demers and Weatherhead, 2001; Wisler et al., 2008). Edges may provide better thermoregulation, cover, and feeding opportunities that make these locations more favorable than interior locations. Therefore, we posit that Giant Gartersnakes will use the edge of emergent vegetation patches more often than is expected based upon its availability.

Our hypotheses that snakes in agricultural areas will have larger home ranges, high temperatures will limit daytime habitat availability, microhabitat use is influenced by vegetation composition, and snakes will use patch edges more than interior locations were evaluated using a single population of threatened Giant Gartersnakes occupying both agricultural and constructed wetlands. We employed radio-telemetry methods to understand snake movements and physical models to describe the thermal environment. Knowledge of Giant Gartersnake spatial ecology will better inform managers of the effects of current landscape structure and give insight into habitat management for a threatened species living within a matrix of agricultural and wetland habitats.

MATERIALS AND METHODS

Study site.—We conducted our study at Gilsizer Slough, which is located in the Sacramento Valley of California, approximately 16 km WSW of Yuba City. This area has been greatly modified by intense agriculture (USDI, 1994) yet is also a focus of conservation planning for the Giant Gartersnake. Over 120 ha of wetlands have been reconstructed since 2003. The study site encompassed 250 ha, which included these constructed wetlands, adjacent rice agriculture, associated drainages and a natural slough (Fig. 2).

***Capture and tagging.*—**We captured Giant Gartersnakes opportunistically by hand or in unbaited floating minnow traps (Casazza et al., 2000). Traps were set May – September in three consecutive years (2007 – 2009). Snakes were captured throughout this period, and we measured snout-vent length, total length, and mass; determined gender; and uniquely marked all snakes with both passive integrated transponder (PIT) tags and microbrands (Winne et al., 2006). Snakes with mass greater than 180 g were removed from the field for radio transmitter implantation, and all others were released after processing. This size restriction limited the scope of our study to adult females because male Giant Gartersnakes are much smaller than females (Wylie et al., 2010). Snakes were anesthetized with Propofol intravenously and implanted with temperature-sensitive radio transmitters (SI-2T, 13 g, 18 – 24 mo battery life or SI-2T, 9 g, 6 – 18 mo battery life; Holohil, LTD) following standard techniques (Reinert and Cundall, 1982). We allowed individuals to recover in captivity following surgery for two weeks or until the skin was shed, whichever came first, and then released them at their capture location. Snakes in captivity were held in individual terraria and fed daily except 24 hours prior to, and 72 hours post, surgery. We captured American bullfrog (*Lithobates catesbeianus*) larvae and small fish at the field site and fed them to the captive snakes. We administered post-operative antibiotics (Baytril) and analgesics (Meloxicam) for three days and kept snakes out of water for 24 hours post surgery. We did not expect any captivity effects because of limited interaction with the snakes. We monitored snake movement closely for the first days following release and did not include the first

10 days post-release in our analysis in case there were any short-term behavioral effects (Withey et al., 2001).

Radio-telemetry.—Snakes were tracked May through September, which is the active period after the mating season, in 2008 and 2009. For females, this encompassed feeding after the anorexic periods of over-wintering and mating, gestation, parturition and late season feeding. We used portable Advanced Telemetry Systems R4000 receivers (ATS, Isanti, MN) and handheld three-element Yagi antennas to obtain locations of the snake from a distance of 3–10 m. Geographic locations were recorded using eTrex and GPS 12 handheld global positioning sensors (accurate to 3–15 m; Garmin Ltd., Olathe, KS). We tracked individuals 5-7 days per week and varied the time of day that we located individuals during daylight hours.

When an individual was located, we measured habitat composition within a 0.5 m radius around the snake. If the snake was within a patch of emergent vegetation, then distance from the snake to the edge of the patch was measured. We defined a patch as any monoculture of emergent vegetation (tules, cattails, primrose, or rice) at least two meters in diameter, and distance was measured on an integer scale up to 10 m (whole numbers 0–10 m). Accuracy of the distance measurement was uncertain for estimates greater than 10 m, therefore we used a single category (> 10 m) to encompass these estimates.

We paired a random point with each snake location to compare used and unused sites. Random points were located from two lists of random numbers generated in Excel: a random uniform compass heading (1–360°) and a random uniform distance 3–

53 m. The random distance range was based upon average daily movement estimated from previous monitoring activities, and our maximum random distance was equivalent to the 75th percentile. We took the same habitat measurements at the random location as at the observed snake location. To better characterize the aquatic environment which is heavily used during the active season, we restricted random points to the same aquatic condition. That is, if the snake was observed in water (including flooded emergent vegetation), then the random point was restricted to water. The opposite held as well: if the snake was observed in dry habitat, the random point was in dry habitat. If the aquatic condition of the random point was not the same as the snake location, then we took a new compass bearing and distance.

Operative temperature models.—In the 2009 season, we assessed the thermal quality of macrohabitats at Gilsizer Slough by making physical operative environmental temperature models. Operative environmental temperature (T_e) is an estimate of the body temperature an ectotherm would experience if it were not actively thermoregulating (Hertz et al., 1993). The physical models were constructed to have thermal qualities similar to that of an adult Giant Gartersnake and used to estimate T_e under various amounts of cover within each macrohabitat. We cut 25 mm diameter copper pipes to 130 mm in length and painted them to give a similar reflectance to the Giant Gartersnake (Peterson et al., 1993). An iButton (DS1921G, accuracy ± 1° C; Maxim Integrated Products, Sunnyvale, CA) was suspended in the middle of the pipe using small pieces of Styrofoam, and rubber stoppers were used to plug both ends of the pipe (Fig. 3).

To test the models for accuracy, we compared temperature readings with a live snake recovering from radio implantation surgery. We placed the model, set to record temperature every minute, inside the terrarium with the snake and moved the terrarium to a protected location in ambient sunlight. In order to calculate the snake's body temperature we used the individual calibration curve of pulse rate versus temperature supplied for each transmitter. We measured the time with a stopwatch for 11 pulses (10 intervals) from the implanted transmitter every minute for the first five minutes and then waited five minutes. We did this for 30 minutes, resulting in 4 temperatures which were then compared with the temperatures recorded on the iButton inside the physical model.

We placed 35 models throughout the study site within the three macrohabitats (terrestrial, emergent, and open water). This included placing the models fully exposed on bare ground, in varying densities of emergent and terrestrial vegetation, under litter (both emergent and terrestrial macrohabitats had litter) and floating exposed on the water surface. Percent vegetation was measured within a 0.5 m radius surrounding the models. The iButtons recorded temperature every 30 minutes.

DATA ANALYSIS

Home range analysis.—We defined an individual's habitat as either agricultural (rice fields and associated drainages) or wetland (constructed wetlands and slough). We used fixed kernel methods (Worton, 1989) to estimate the areas encompassed by the 50% and 95% density contours, hereafter called the core area and home range area, respectively

(White and Garrott, 1990; Bingham and Noon, 1997). The smoothing parameter was calculated by the reference method as neither least squares cross-validation nor likelihood cross-validation methods converged for all individuals in the analysis. Fixed kernel estimates using the reference method to calculate the smoothing parameter have been shown to be better estimators for animals with linear home ranges (Blundell et al., 2001), and earlier observations suggested that snake movements within agricultural habitat were linear. In rice fields, snakes followed field edges and berms, and in drainages they were limited to linear movements up and down the drain. All locations were included except when a snake was caught in a trap and for the first 10 days after an individual was released following recovery from transmitter implantation surgery. This was done to remove any possible post-captivity behavior (Withey et al., 2001).

To ensure estimates of home range and core areas were robust to the number of locations sampled, we ran area-observation curves for each individual (Kernohan et al., 2001). This was done by subsampling the locations of each individual and estimating the home range size from the subsample. Subsamples began at 10 locations and increased by 5 locations until the maximum number of locations for an individual was reached. We visually assessed the curves and assumed the home range estimation to be robust if the plot reached an asymptote.

We estimated the percent cover of the three macrohabitat types at our field site (terrestrial, emergent, and open water) within each home range for both years. This was done in ArcMap (ver. 9.2, ESRI, Redlands, CA) using NAIP imagery for the agricultural habitat and aerial images taken by Wildlands, Inc. for the wetland habitat.

From these images, we created polygons of the macrohabitats and used Hawth’s Tools (ver. 3.27, Beyer, 2007, http://www.spatialecology.com/htools/index.php) to calculate the area of each polygon within each home range 95% contour.

Home range overlap was estimated using the Utilization Distribution Overlap Index (UDOI; Fieberg and Kochanny, 2005). This static interaction analysis compares two individuals’ home ranges and assumes independence of space use between the individuals. It measures the degree of overlap as well as the similarity in utilization distributions in the overlapping area. The UDOI has been shown to be more effective in capturing this relationship than both the Bhattacharyya’s Affinity and the volume of intersection statistic (Fieberg and Kochanny, 2005).

The descriptive, non-experimental nature of our study allowed us to use boxplots to visually compare the percent of macrohabitats within home ranges and the distribution of home range sizes between agricultural and wetland habitats. We were also interested in estimating the difference in size of home ranges, and in this case, Johnson (1999) suggested the use of confidence intervals as a more insightful method of data interpretation. Therefore, confidence intervals from a general linear model were used to compare mean core and home range sizes between the two habitat types. We used means and standard errors to compare average home range overlap.

Thermal quality analysis.—We investigated the daily patterns in T_e for each gestational period during the active season (early, late, and post gestation) and macrohabitat type (terrestrial, emergent, and open water). Early, late, and post gestation were defined as May 1 – June 30, July 1 – August 15, and August 16 – September 30, respectively. A mean T_e was estimated for the physical operative temperature models in each season and macrohabitat as well as each hour of the day encompassed by the telemetry study (8:00 h – 19:00 h).

To better explain the extent a snake would have to thermoregulate in each macrohabitat, we calculated the thermal quality index (d_e). This is the mean deviation of T_e from the species preferred body temperature (T_{set}) (Hertz et al., 1993). For the Giant Gartersnake, the field preferred body temperature was estimated to be 29.8° C with a range of 27.6° C to 31.7° C (Wylie et al., 2009), and we assumed this to be equivalent to T_{set}. To estimate d_e from the mean T_es, the range of T_{set} was used following the equations below:

$$\text{if } T_e < 27.6, \text{ then } d_e = 27.6 - T_e$$

$$\text{if } 27.6 \leq T_e \leq 31.7, \text{ then } d_e = 0$$

$$\text{if } T_e > 31.7, \text{ then } d_e = T_e - 31.7$$

We estimated mean d_e as we did T_e, separated by gestational period, macrohabitat and hourly during the day and also calculated the percent time that $d_e = 0$ (T_e was within T_{set}).

Habitat selection analysis.—We analyzed habitat use with a case-control design because our data was collected using a 1:1 matched pair design. For every snake observation, one random point was immediately located (as detailed above). We assumed that use by snakes was rare on the landscape, therefore we could consider the random locations to be true absences (Keating and Cherry, 2004; Duchesne et al., 2010). Conditional mixed logistic regression was used to investigate habitat use as a function of vegetation composition. We used standard generalized linear mixed-effect regression software because our design was a 1:1 case-control (Hosmer and Lemeshow, 1989). We took the differences between observed and random locations for each category and regressed with a response always equal to one using a binomial distribution (logit link). In this form, the model does not have an intercept. The individual snakes were incorporated into the model as a random effect, which allowed us to analyze variation among individuals in the population by looking at the standard deviation of the random variable.

Three separate habitat use models were fit, one for each of the three gestational periods in the active season (early, late, and post-parturition). Because of our small sample size of individuals, we chose a few *a priori* models limited to two fixed effects for each period. We included terrestrial, emergent non-rice, emergent rice, bare ground, and open water as microhabitat variables. Rice was not included in the early gestation period because it is being seeded and in the very early stages of growth during this period. The one and two fixed-effect variable models were compared using Akaike's Information Criterion (AIC) as guidance for balancing model fit with complexity (Burnham and Anderson, 2002; Zuur et al., 2009). The model with the lowest AIC value was considered "best" and any models within two units of the best model were considered competitive.

The last analysis we performed investigated snake use of vegetation patch edge versus the interior. We gathered all the data pairs for which both observed and random locations were within a patch. We defined the edge of a patch as between 0 – 3 m, and interior was 4 m or more from the edge. To keep the conditional design, we ran a generalized linear mixed model on the counts of each of the four combination types (both at patch edge = EE; observed at edge, random interior = EI; IE; and II). A Poisson distribution was assumed a good approximation for these data and the following was our full model:

$$C_{ij} \sim P_{ij} + I^{0}_{i} + I^{1}_{i}\,(P_{ij}) + \varepsilon_{ij}$$

C_{ij} is the count of the j^{th} combination of the i^{th} individual

P_{ij} is a categorical variable describing the combination of observed/random locations of the i^{th} individual; $j = 1 – 4$ (EE, EI, IE, II)

I_i is a random variable describing the i^{th} individual; $i = 1,2,\ldots,9$

$$\begin{bmatrix} I^{0}_{i} \\ I^{1}_{i} \end{bmatrix} \sim N(0,\sigma_{I}^{2})$$

Individual was included as a random effect, and AIC was used to compare full and reduced models.

The open-source software, R 2.11.1 (R Development Core Team, Vienna, Austria, http://www.r-project.org), was used for all statistical analyses. We used the adehabitat package (Calenge, 2006) for home range estimations and overlap analyses and lme4 package (Bates and Maechler, 2010) for all mixed-effect models.

RESULTS

We radio-tracked a total of 19 unique female snakes, with five of these snakes tracked in both the 2008 and 2009 seasons (Table 1). Thirteen snakes were tracked in 2008, during which we had two radios fail and one snake die of unknown cause. In 2009, we tracked 11 snakes and had one death because of a collapsed burrow. Snakes were included in the home range analyses as determined by the area-observation curves and in the 2009 habitat selection analyses if a snake had greater than 10 locations within the season or gestation stage of interest.

Home range and core area size.**—**In both years, we found that snakes in wetland habitat had larger and more variable core area and home range sizes than snakes in agricultural habitat (Fig. 4). After visually assessing the area-observation curves, we assumed home range estimates were robust over 40 locations (see Fig. 5). The curve of one individual with 32 locations did not reach an asymptote and we excluded her from analyses. All other snakes had greater than 40 locations and were included in the analyses. Twelve snakes were included in the 2008 analyses, six in each habitat type, and eleven snakes were included in the 2009 analyses, six in wetland and five in agricultural habitats (Table 1).

Mean core areas were much smaller in agricultural habitat than in wetland habitat. We estimated mean core area to be 3 ha for snakes in agricultural habitat and 20 ha for snakes in wetland habitat in 2008 (Table 2, Fig. 4). Mean core area of snakes in wetlands was 0 – 33 ha larger (95% confidence interval) than the mean in agricultural habitat. In 2009, mean core areas were estimated to be 1 ha and 7 ha for snakes in agricultural and wetland habitats, respectively. Mean core area of snakes in wetlands were 0 – 11 ha larger (95% confidence interval). In both years, there was little variation in mean core area among snakes in agricultural habitat (Fig. 4).

Home ranges followed a similar pattern to core areas, with mean home range size much smaller in agricultural than wetland habitat. In 2008, the mean home range of snakes in agricultural habitat was 13 ha and 77 ha for snakes in wetland habitat (Table 2, Fig. 4). We estimated mean home ranges in the wetland habitat to be 0 – 127 ha larger (95% confidence interval) than those of snakes in agriculture. In 2009, mean home ranges were estimated to be 7 ha and 31 ha in agricultural and wetland habitats, respectively. The mean home range of snakes living in wetland habitat were 2 – 46 ha larger (95% confidence interval) than those in agricultural habitat. Mean home range size was more variable for snakes in wetland habitat in both years (Fig. 4).

***Home range composition*.**—Home ranges had similar percentages of the macrohabitats in both wetland and agricultural habitats, but there was some variation in the estimates (Fig. 6). In both years, water was on average 5% of snake home ranges in agricultural habitat and 13% of snakes in wetland habitat. Mean percentage of terrestrial and emergent macrohabitats within home ranges was not consistent between 2008 and 2009. For snakes in agricultural habitat, terrestrial macrohabitat averaged 43% and 49% in 2008 and 2009, respectively. In 2008, the mean percentage of terrestrial macrohabitat for snakes in wetland habitat was 42%, and in 2009, it was 32%. Emergent macrohabitat averaged 42% and 41% of home ranges for snakes in agricultural habitat in 2008 and 2009, respectively. Mean percentage of emergent macrohabitat for snakes in wetland habitat was 38% in 2008, and 50% in 2009.

***Home range overlap*.**—There was greater and more uniform home range overlap in the agricultural snakes than the wetland snakes as evidenced by the UDOI (Table 2 and Fig.

7). A UDOI of zero indicates no overlap between two individuals, 1 indicates complete overlap with uniform distributions (two snakes are using the exact same area in the exact same way), and greater than 1 indicates a high degree of overlap, but non-uniform distributions. Agricultural snakes had similar overlap indices in both 2008 and 2009 (Table 2), with mean 0.46 (0.16 – 0.77, 95% CI) and 0.42 (0.21 – 0.63, 95% CI), respectively. Wetland snakes had a mean index of 0.26 (0.14 – 0.37, 95% CI) in 2008 and 0.17 (0.05 – 0.30, 95% CI) in 2009.

Thermal quality.—Emergent habitat had a mean T_e that was always within or just below T_{set} (Table 3), while mean open water T_e was consistently below T_{set} and mean terrestrial T_e was consistently above T_{set}. Emergent and open water were similar in their thermal quality as described by the percent time d_e was zero (19-20% for both habitats throughout the season). Thermal quality was on average the lowest in terrestrial habitat, but fully exposed models in both terrestrial and emergent habitat reached extreme temperatures.

When we looked more specifically at the daily trends in temperatures and thermal quality, we found that all three gestation periods were very similar (Fig. 8). Environmental temperatures in open water and emergent vegetation were close, if not within, the field preferred body temperature of the Giant Gartersnake for most of the day (Fig. 8A). A better representation of the difference in temperature from preferred is the daily trends in thermal quality (Fig. 8B). The early morning and late evening thermal quality is similar among all macrohabitats, but a great difference in thermal quality occurred in the afternoon peak temperatures. In the afternoon, differences in average thermal quality between terrestrial and other habitats could be as high as 10° C.

Habitat selection.—All females but one were gravid in 2009. Non-gravid females select habitat differently than gravid females because of differing thermoregulation requirements (Charland and Gregory, 1995; Blouin-Demers and Weatherhead, 2001); therefore we excluded the non-gravid female from these analyses. This resulted in a sample size of ten snakes in the early gestation period and nine snakes for the other two periods (one snake died in the beginning of the late gestation period).

All single-variable models were considered competitive based upon their AIC values, and no two-variable models were selected because of their higher AIC values. All vegetation parameters in the selected models were similar to the odds of 1 (Table 4), suggesting a lack of selection. The small differences in means observed would likely not be biologically significant, even if found to be statistically significant. There was a large amount of among-snake variation (random effect SD = 22 – 23 in all gestation stages) indicating that our model structure did not explain all of the variation.

Adult female Giant Gartersnakes used the edge of vegetation patches more often than interior locations. The full model was selected with the location combination as both a fixed effect and random slope, but a model with the combination as only a fixed effect was closely competitive (Table 5). The full model indicates that each combination of observed and random locations has different odds of being selected but the difference in odds varies by individual. Both the observed and random location at the edge of a patch (EE) and the observed at the edge and random in the interior (EI) had the highest odds of being chosen. Namely, a location at a patch edge had double the odds of a snake using that location when compared to interior locations. To understand individual variation in this model, we compared the standard deviation of the random effect (individual) to the magnitude of the fixed effect (location combination). The among-snake variability was fairly small when edge locations were used, but there was a large amount of variability when interior locations were used (Table 6).

DISCUSSION

We found that Giant Gartersnakes in agricultural habitat exhibited more restricted movements than snakes in wetland habitat. Home range results were contrary to our predictions: snakes in agricultural habitat had smaller, less variable home range and core areas with more overlap between individuals than snakes in wetland habitat. This could be a reflection of lower amounts of suitable habitat and a high degree of fragmentation, although we do not have the data to support a mechanism for these observed differences. Our description of the macrohabitat thermal environment showed differing conclusions dependent upon which time scale was used. Seasonal temperature means indicated a benign thermal environment, yet hourly means showed extreme afternoon temperatures on the surface of terrestrial habitat. These extremes may restrict Giant Gartersnakes to use of emergent, water, or underground habitats during this time of day. We also found adult females select edges of emergent vegetation patches which may affect management of wetland vegetation and the consideration of rice fields as suitable habitat.

When trying to relate optimal versus suitable habitat for a species based upon movement observations, it is important to understand that many mechanisms influence these patterns. Food availability, land-use practices, habitat type, and individual differences are possible mechanisms of intraspecific variation in home range size (Ebersole, 1980; Tufto et al., 1996; Borger et al., 2006; Vila et al., 2008). Snakes in agricultural habitats could exhibit smaller ranges because the habitat adequately meets their requirements (Tufto et al., 1996; Pasinelli et al., 2001). However, the lack of variation and increased space use sharing between individuals observed at Gilsizer Slough suggests there is a lack of suitable surrounding habitat. The restricted snake ranges in agriculture are likely because of the high costs associated with movement between suitable habitats or the inability to perceive the next patch of suitable habitat (Pasinelli et al., 2001; Morris, 2003; Rhodes et al., 2005).

Our observations from trapping and foot-searching for Giant Gartersnakes along the drainages spanning Gilsizer Slough indicate that snakes rarely used the drainage which structurally links the agricultural and wetland habitats (Fig. 2). This 800 m stretch of drain is unvegetated, and while we did see occasional exploratory movements by snakes with transmitters in this area, they quickly returned to previous locations and never traveled far enough to reach the next area of drainage that is vegetated and close to the wetlands (P. Valcarcel, pers. obs.). These observations lend support to our findings that Giant Gartersnakes in the agricultural areas of Gilsizer Slough area are exhibiting a fusion response to local scale fragmentation (Ims et al., 1993; Verbeylen et al., 2009).

Pattishall and Cundall (2008) found that Northern Watersnakes living in an urban stretch of stream exhibited reduced movements and higher fidelity to sites compared to snakes living along natural stretches of the same stream. They concluded that higher mortality associated with the urban areas was a possible cause of reduced snake movements in urban stretches. We observed a similar difference in survival between our snakes living in agricultural and wetland habitat. We had a total of 12 mortalities and 11 of those mortalities occurred within agriculture associated habitat. Ten of 15 (67%) radio-tagged snakes in agricultural habitat died whereas only 2 of 11 (18%) wetland associated snakes died and one of those deaths occurred while the snake was overwintering in the drainage/agricultural area. This high risk of movement for snakes in agricultural habitat is a possible reason for the restricted movements observed in snakes in this area. The lack of emergent vegetation cover within the drainage surrounding the area used by the radio-tagged snakes could be perceived as too risky and create a loss of functional connectivity between suitable habitats.

We also observed a large amount of variation in home range sizes between the two years of our study. In 2009, home ranges were smaller than in 2008, regardless of habitat type. Additional wetlands were being constructed in late spring and early summer of 2009, which caused the land managers to lower the water in the wetlands. This decreased amount of available water for the early part of the Giant Gartersnake active season would not have affected the snakes living in agriculture or those utilizing the slough. Monthly average temperatures were similar between years, although it is possible there was higher rainfall or increased cloud cover in 2009. Therefore, it does not appear to be management related or temperature related. With only two years of data, we cannot know if this is within a normal level of inter-annual variation.

Our study described another aspect of habitat suitability for reptiles: temperature. We found that considering only the seasonal average temperature of macrohabitats results in a different conclusion than considering the hourly averages and extremes. Seasonal temperature means and daytime averages indicate a thermally benign environment. Wylie et al. (2009) came to a similar conclusion while investigating Giant Gartersnake body temperatures. Although it may be true that the Central Valley is a thermally benign environment on average, our results demonstrate that afternoon temperatures are extreme enough to restrict snake use to emergent, water, or underground habitats. Thermal sensitivity studies of a montane California gartersnake (*Thamnophis elegans*) showed that its voluntary thermal maximum was 36° C and critical maximum was 43° C (Scott et al 1982; Stevenson et al. 1985). At our field site, the seasonal means in terrestrial habitat were 35.1 – 37.6° C, which may be at, or near, the voluntary thermal maximum of the Giant Gartersnake, and maximum temperatures were as extreme as 72.2° C for fully exposed models. Therefore, we need to consider available habitat as changing over the course of a day when analyzing microhabitat use (Arthur et al., 1996) because of the extreme afternoon temperatures. We also noted the importance of cover in this environment as extreme temperatures were observed in all three macrohabitats when individual models were fully exposed. This is likely a result of the typically cloudless summers in the Central Valley leading to high solar radiation. Therefore, cover in any habitat type not only plays a role in protection from predation but also in regulating snake body temperature.

Structure of vegetation, such as stem densities or plant physiognomy, within the macrohabitat may also play an important role. Our analysis of Giant Gartersnake use of vegetation patch edges showed that adult females used edge more often than interior locations. A location at the edge of a patch almost doubled the odds of a snake using that location compared with the interior. We defined edge as 0 – 3 m; therefore, our results indicate that complex habitat with many small patches (less than 6 m in diameter) are likely more suitable than large patches dominated by a single species of emergent vegetation. Though our data only investigated use once snakes were within a patch and did not look at edge use versus overall availability, it was rare to observe snakes in unvegetated water. When we did observe snakes in open water, they were always moving (P. Valcarcel, pers. obs.). Greater use of edges could be a result of many factors, including optimal thermoregulation, cover from predation, and feeding opportunities that make these locations more favorable than the interior of patches. Conservation planning for the Giant Gartersnake must take this into account as it will change how we manage and restore habitat for this species. This is true not only for the consideration of rice fields as suitable habitat but also wetland management. In many areas, wetlands that are not maintained can become overgrown with tules, cattails, and the invasive primrose, creating extremely dense patches over 100 m in width. Based on our finding of greater use of edges, this overgrowth in wetlands would not provide optimal habitat for the Giant Gartersnake.

We were unable to detect a difference in microhabitat use related to habitat composition, although we did observe adult female Giant Gartersnake use of macrohabitats change over the day. Therefore, the lack of a difference at the microhabitat level could be a result of scale. We attempted to look at a finer scale of selection and account for possible changes in availability throughout the day as discussed above, but because of our small sample size we did not include time of day in the analysis. Our random points were restricted to similar water status as the snake location in order to exclude terrestrial habitats or dry emergent habitat if high temperatures had caused the snake to choose a flooded environment. The lack of our detecting selection may have been due to the small spatial scale. If Giant Gartersnakes do exhibit non-random use at this scale, they may not select habitat based upon composition; microhabitat use may be more influenced by stem densities or the physiognomy of the vegetation.

Management implications.**—**The current design of rice agriculture may result in suboptimal habitat for Giant Gartersnakes because adult females used the edge of dense patches much more than interior locations. This limited use of patch interiors severely decreases the amount of functionally available emergent vegetation to Giant Gartersnakes living in agricultural habitats. This, coupled with extreme afternoon temperatures that limit use of surface terrestrial habitat, may explain some of the restricted movements we observed in snakes living in agricultural habitat. Further, the habitat to which agricultural snakes are restricted is simple, consisting of linear drainages and rice field edges characterized by large gaps between vegetation structures, and simple habitats have been known to increase predator effectiveness (Gotceitas and Colgan, 1989; Butler and Gillings, 2004; Warfe et al., 2008). Therefore, the limited, simple habitat may partially be the cause of the higher mortality we witnessed for Giant Gartersnakes living in agricultural areas.

Another concern for conservation planners is the dispersal of Giant Gartersnakes into constructed wetlands. If the restricted movement we observed in snakes in rice agricultural habitat at Gilsizer Slough is reflective of Giant Gartersnakes in agricultural areas, some constructed wetlands may not be colonized despite their close proximity to Giant Gartersnake populations. It is possible that local fragmentation in the agricultural drainages is a cause of the restricted movements at our site, and perhaps drainages could be maintained in a manner that retains connectivity. Currently, drainages are managed to limit vegetation within the drain to maintain water flow, and areas without vegetation may be acting as a barrier to Giant Gartersnake dispersal.

As we gain knowledge of the importance of patch edges and habitat complexity, rice agriculture as suitable primary habitat for the Giant Gartersnake comes into question. Although rice fields and surrounding drainages should not be discounted as habitat for the Giant Gartersnake, conservation planners may need to reconsider its role as primary habitat and improve connectivity through changes in drainage management to help sustain the current subpopulations. The importance of habitat complexity also applies to wetland management. As stated above, many wetlands that are not managed can become overgrown with native and non-native plants, such as tules, cattail, and primrose. These species can out-compete other species and create a similar situation to the rice fields: one large patch dominated by a single species. If this occurs, the amount of edge habitat and structural complexity is reduced. Land managers should maintain emergent vegetation such that it retains complexity with many smaller patches and a variety of species.

Limitations.—Although we had a small sample size of individuals, we believe it was representative of adult females at this site. However, conclusions beyond this single population cannot be drawn. This was an observational study from which we cannot infer causation nor the mechanisms of Giant Gartersnake movement. With only one site of each habitat type (agricultural and wetland), we cannot confirm whether our observations at Gilsizer Slough are typical of all Giant Gartersnakes living in similar habitats, or if these results are because of site-specific differences in habitat type. The sampling effectiveness of Giant Gartersnakes in agricultural drainages is likely higher than in wetlands (P. Valcarcel, pers. obs.); therefore it is possible that we caught a higher proportion of individuals in the agricultural habitat. This could be another reason for the appearance of more space use sharing between individuals. We also do not have the data to support whether the restricted movements observed in adult females living in agricultural habitat were because the area is of high quality or a high degree of fragmentation. Personal observations of prey distributions and mortality suggest fragmentation may be the cause but an adequate research design will be needed to fully address this question. Research into prey abundance and distribution would be extremely valuable information as these are likely major determinants of snake movements during the active season (Johnson et al., 2007; Halstead et al., 2009;

Indermaur et al., 2009). Data on movements of juvenile and male Giant Gartersnakes are also lacking. It may be that adult females are more sedentary and establishment of created wetlands would occur through dispersal of juvenile snakes.

Another large caveat is the assumption in studies utilizing radio-telemetry that transmitters do not impact the behavior of individuals. Recent research into the histological and pathological effects of surgically implanting transmitters into snakes concluded that this assumption may be invalid (Lentini et al., 2011). One third of their subjects developed extensive inflammation and bacterial infections from the transmitters, and another third developed mild inflammation but did not develop infections. Therefore, inflammation in response to the implanted transmitters is likely. Although there is a lower probability of infection, the inflammation could affect the individual's behavior and influence survival. Giant Gartersnakes in agricultural habitat have lower body condition than those in the less disturbed wetlands (Wylie et al., 2010), and the additional stressor of the transmitter could make these snakes more susceptible to complications with the transmitter or increase their mortality risk. The behavior of the snakes in the two habitat types did not appear to be different based upon our personal observations, but this possibility should not be overlooked.

Given the Giant Gartersnake's conservation status and habitat restoration occurring as part of management planning, it is extremely important we understand the mechanisms underlying its space use. More research is needed to draw more definitive conclusions for effective habitat planning and conservation for this species. The secretive nature of this snake made the use of radio-telemetry extremely beneficial, but noting the possible complications, less invasive procedures should be utilized in future studies of this sensitive species. Our research improved knowledge of Giant Gartersnake ecology and will inform management, despite these limitations.

ACKNOWLEDGEMENTS

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FIGURES

Fig. 1. California rice producing counties and counties with observed Giant Gartersnake populations. Rice and wetlands in which the Giant Gartersnake lives only occur in the Central Valley (outlined on the maps). Subpopulations of the Giant Gartersnake overlap with rice producing counties, and stable subpopulations reside in the main rice production areas.

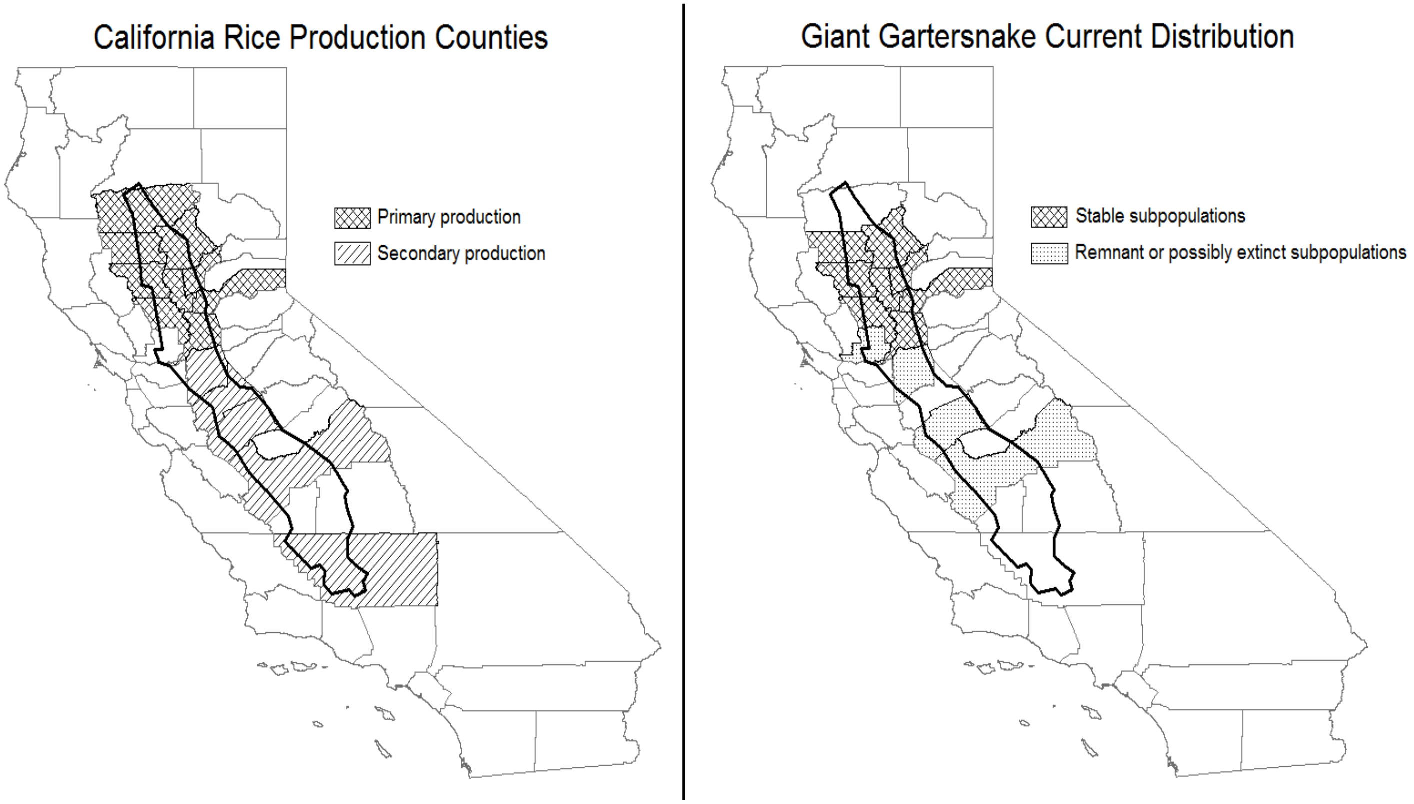


Fig. 2. Gilsizer Slough in 2006 with agricultural (rice) and constructed wetlands. The constructed wetlands are outlined by the solid line and the rice fields are outlined by the dotted line. The dashed line follows the main drainage which flows south along a levee and indicates the southern and western border of our site.

Fig. 3. Physical model recording the operative environmental temperature of an adult Giant Gartersnake. Small pieces of Styrofoam hold the iButton suspended in the middle of the pipe allowing air to flow between both halves.

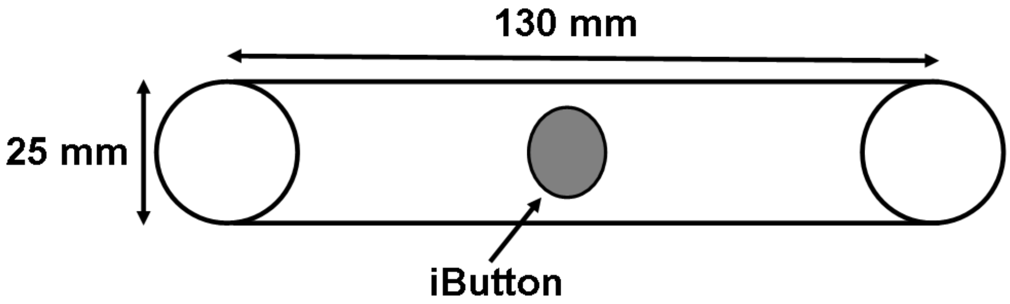


Fig. 4. Adult female Giant Gartersnake core area and home range sizes by habitat type in 2008 and 2009. The median is the bold line within the box.

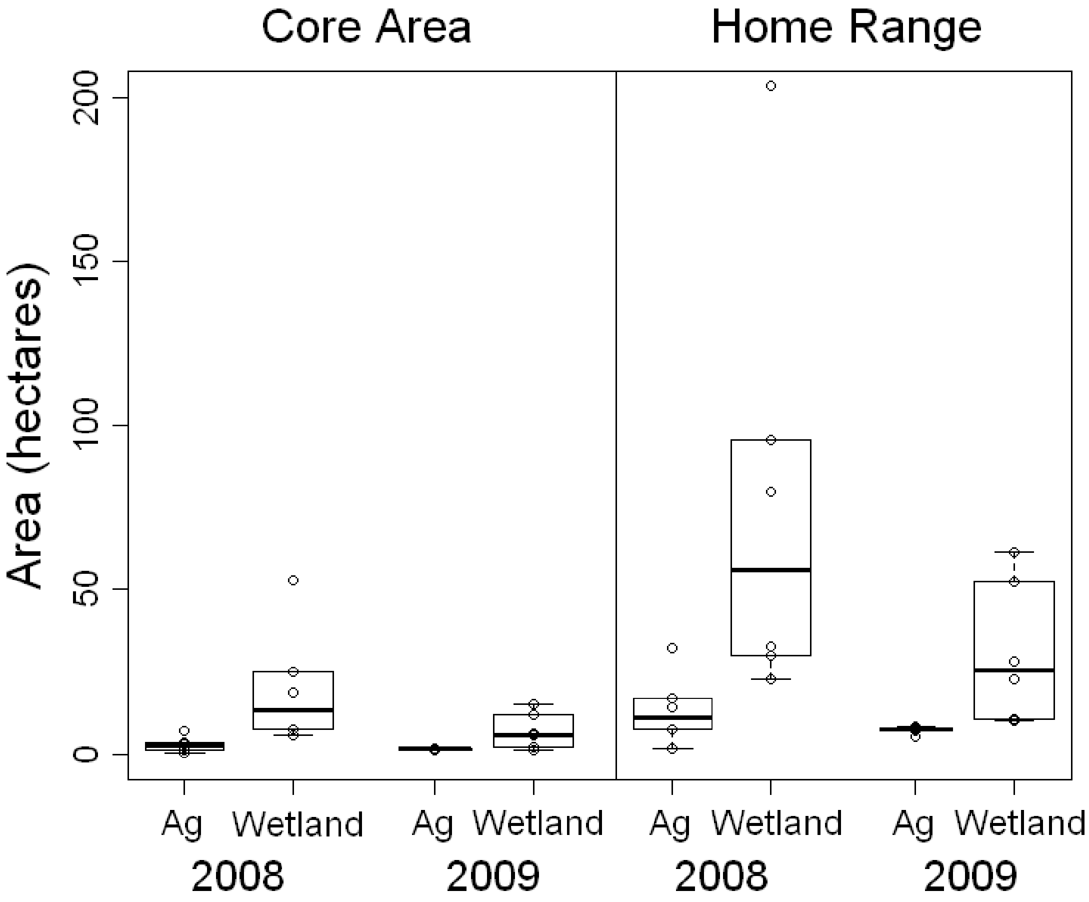


Fig. 5. An example of area-observation curves used to visually assess robustness of home range estimates. The locations for each individual were subsampled (n = 20) and home range estimates of the subsampled points plotted (A) along with the means of each group (B). A home range was assumed to be robust if variation between sequential means was less than 5 hectares. The snake shown below would be considered to have a robust estimate over 55 locations, but most snakes had robust estimates after 40 locations.

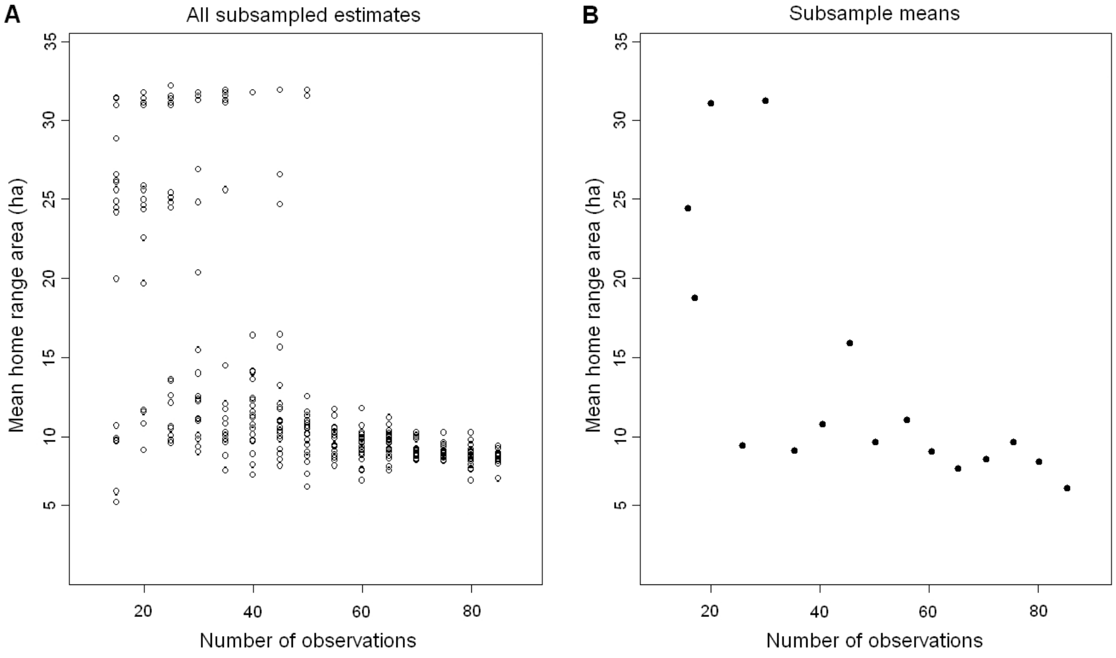


Fig. 6. Percentage of the three macrohabitat types within home ranges in 2008 and 2009. The whiskers of the boxplots extend to the most extreme point that is at most 1.5 times the length of the box. The median is the bold line within the box.

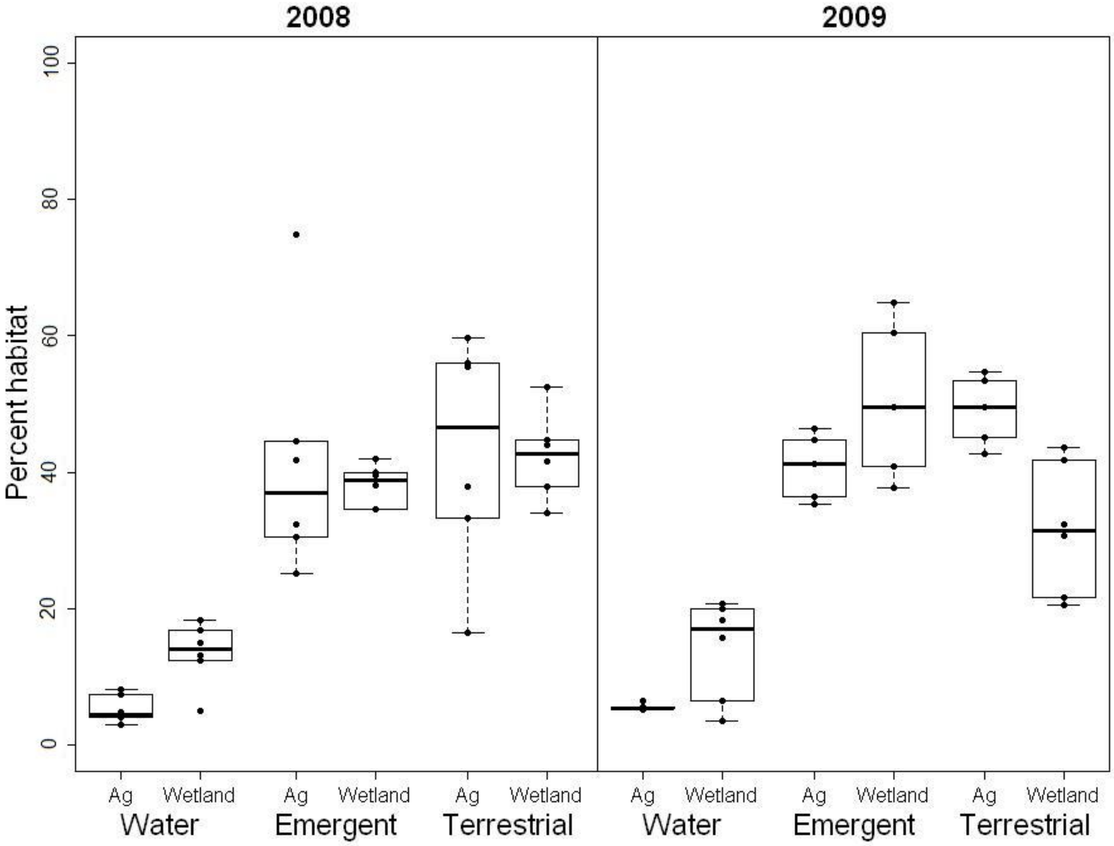


Fig. 7. Home range overlap and Utilization Distribution Overlap Index (UDOI) in 2008 and 2009. The shading of home ranges increase with increasing number of overlapping individuals. The solid line encircles the snake home ranges in agricultural habitat and the dotted line encircles snakes in wetland habitat. There is a higher concentration, higher degree of overlap, and similarity in UD shapes of the agricultural snakes. The UDOI (mean ± 1 SE) is shown at the bottom of figure.

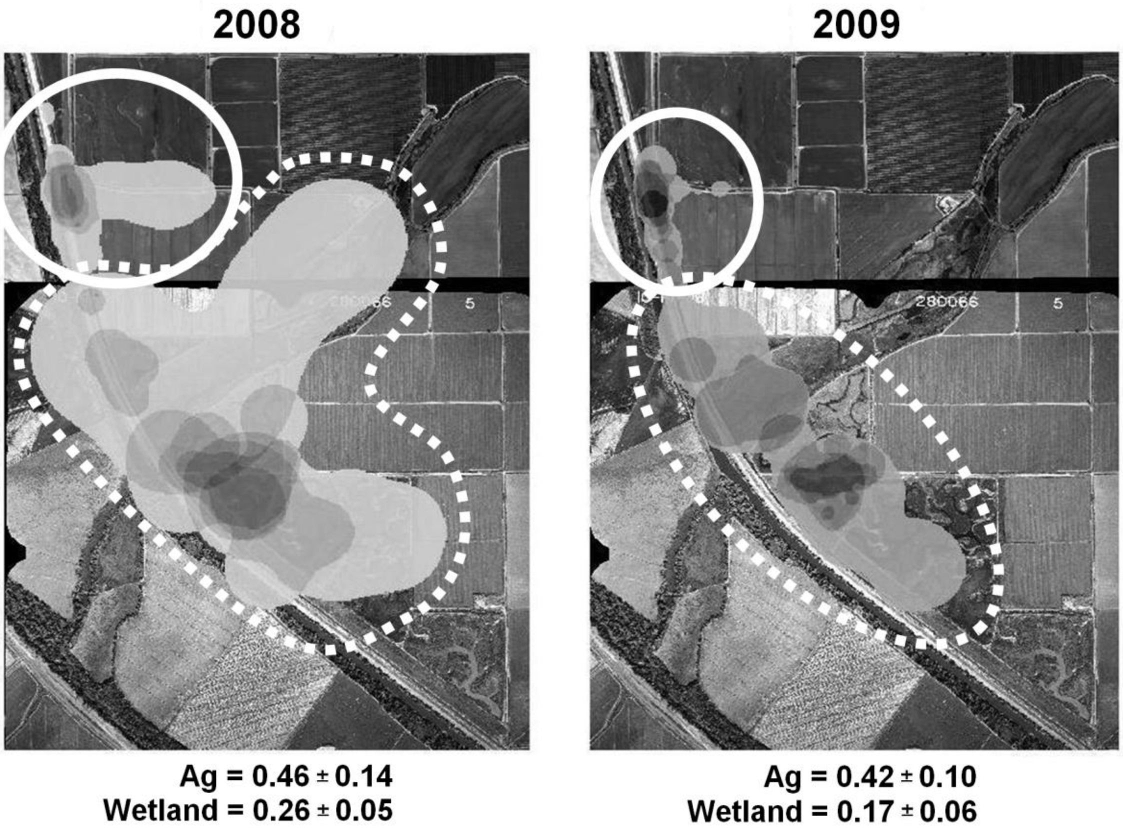
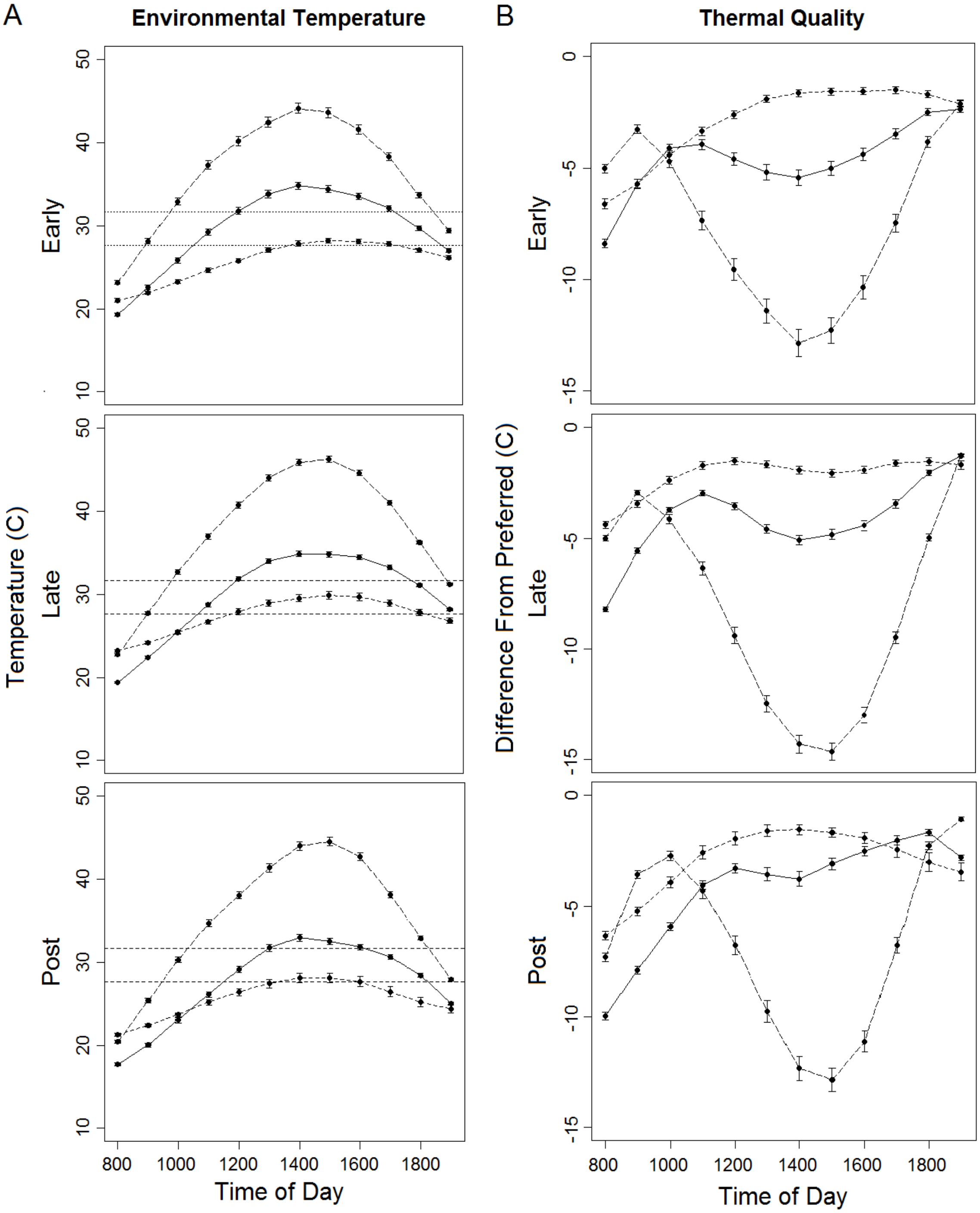


Fig. 8. Hourly averages of temperatures (T_e) and thermal quality (d_e) in each gestation period. Mean operative environmental temperature (A) and thermal quality (B) for each hour of the day covered by the telemetry study. The data are divided by gestation period during the active season (early gestation, late gestation, and post parturition). In A, horizontal dotted lines indicate the range of preferred temperatures of adult Giant Gartersnakes. Negative d_e is plotted to demonstrate thermal quality decreases with increasing distance from 0. Each gestation period is subdivided by emergent (solid line), terrestrial (dashed line), and open water (dotted line) macrohabitats. Error bars show ± 1 SE.

Fig. 8.


A
Environmental Temperature
B
Thermal Quality
Temperature (C)
Early
Late
Post
50
40
30
20
10
Difference From Preferred (C)
0
-5
-10
-15
800
1000
1200
1400
1600
1800
Time of Day

TABLES

Table 1. Snake tracking information and home range estimates. Individuals tracked during the 2008 and 2009 seasons, their habitat type, beginning and end dates of tracking, total number of relocations, and estimates of core (50% kernel) and home range (95% kernel) areas. Asterisks in 2008 indicate that snake died in early 2009 (before the start of the 2009 season), and plus signs indicate that snake was tracked in 2008. Snake 47170C0666 had too few locations and was excluded from analysis.

Year	*PIT*	*Habitat*	*Begin*	*End*	*# Reloc*	*50% (ha)*	*95% (ha)*
2008	470B325A0A*	Agric	5/1/2008	9/30/2008	111	1.9	7.5
	4717220825	Agric	7/29/2008	9/30/2008	43	3.10	16.79
	4719132D51*	Agric	5/1/2008	8/20/2008	75	3.17	14.25
	4719270C06	Agric	5/1/2008	9/30/2008	119	0.27	1.44
	471A204A3D	Agric	5/1/2008	7/2/2008	54	1.20	7.28
	484B6C6E45*	Agric	6/27/2008	9/30/2008	65	7.00	32.31
	445D604B00	Wetland	5/1/2008	9/30/2008	113	7.31	29.76
	456542613E	Wetland	5/1/2008	9/30/2008	91	5.51	22.51
	45763D0A12	Wetland	5/1/2008	9/30/2008	112	18.64	79.92
	47170C780A	Wetland	5/1/2008	9/30/2008	86	25.08	95.47
	4717131A00	Wetland	5/1/2008	9/30/2008	116	7.65	32.58
	4717385C64	Wetland	5/1/2008	9/30/2008	106	53.09	203.52
	47170C0666	Wetland	5/1/2008	6/7/2008	32	-	-
2009	4717220825	Agric	5/1/2009	9/30/2009	125	1.00	5.40
	445D5D4B34	Agric	6/18/2009	9/30/2009	78	1.49	7.89
	471905467D	Agric	5/27/2009	9/30/2009	87	1.73	8.21
	4719270C06$^+$	Agric	6/18/2009	9/30/2009	77	1.09	7.49
	471A204A3D$^+$	Agric	6/18/2009	9/30/2009	71	1.43	7.14
	445D604B00$^+$	Wetland	5/1/2009	7/2/2009	37	5.83	22.81
	451E7F195D	Wetland	5/1/2009	9/30/2009	86	12.04	52.36
	456542613E$^+$	Wetland	5/1/2009	9/30/2009	90	2.11	10.63
	47170C780A$^+$	Wetland	5/1/2009	9/30/2009	87	15.07	61.22
	484F373D20	Wetland	5/1/2009	9/30/2009	75	5.88	28.33
	484F5F107D	Wetland	5/1/2009	9/30/2009	91	1.21	10.24

Table 2. Home range size, core area and overlap of adult female Giant Gartersnakes. Core area is the 50% kernel home range (50% KHR), home range area is the 95% kernel home range (95% KHR), and UDOI is the utilization distribution overlap index. Fixed kernel methods were used to estimate kernel contours. Estimates are mean ± 1 SE.

Year	*Habitat*	*Sample size*	*50% KHR (ha)*	*95% KHR (ha)*	*UDOI*
2008	Agricultural	6	2.78 ± 0.95	13.26 ± 4.42	0.46 ± 0.14
	Wetland	6	19.55 ± 7.40	77.29 ± 28.01	0.26 ± 0.05
2009	Agricultural	5	1.35 ± 0.14	7.22 ± 0.49	0.42 ± 0.10
	Wetland	6	7.02 ± 2.24	30.93 ± 8.74	0.17 ± 0.06

Table 3. Operative environmental temperatures and thermal quality in each gestation period. Mean ± 1 SE operative environmental temperatures (T_e) and associated thermal quality indices (d_e) for each gestation period and macrohabitat. Lower d_e translates to higher thermal quality. Percent time that d_e equals zero (d_e 0) is the percent time that T_e was within the Giant Gartersnake's field preferred body temperature range.

Period	*Macrohabitat*	*Mean T_e*	*Max T_e*	*Min T_e*	*Mean d_e*	*Max d_e*	*d_e 0*
early	emergent	29.55 ± 0.13	61.25	13.75	4.57 ± 0.08	29.55	19
	open water	25.74 ± 0.10	40.25	14.75	2.88 ± 0.07	12.85	21
	terrestrial	36.31 ± 0.17	72.25	16.00	7.53 ± 0.13	40.55	17
late	emergent	29.91 ± 0.09	58.00	14.00	4.14 ± 0.05	26.30	21
	open water	27.42 ± 0.12	38.75	20.00	2.15 ± 0.05	7.60	19
	terrestrial	37.56 ± 0.12	69.25	16.50	8.19 ± 0.10	37.55	15
post	emergent	27.42 ± 0.13	55.50	12.50	4.23 ± 0.08	23.80	21
	open water	25.51 ± 0.17	34.25	19.25	2.98 ± 0.11	8.35	19
	terrestrial	35.05 ± 0.17	64.25	14.00	6.75 ± 0.13	32.55	18

Table 4. Generalized linear mixed-effects model ΔAIC values and estimates for habitat use analysis. All models had individual as a random intercept. Estimates for two-variable models were not assessed because of the higher AIC values. ΔAIC values are from maximum likelihood estimation, whereas the reported estimates are from restricted maximum likelihood estimation. The transformed parameter estimates (± 1 SE) are shown and reflect the change in the odds of a location being used.

Gestation Stage	*Variables*	*Estimate*	*ΔAIC*
Early	Terrestrial	1.001 ± 1.072	0
	Emergent	1.004 ± 1.068	0
	Bare ground	0.988 ± 1.116	0
	Terrestrial + Bare	-	2
	Emergent + Bare	-	2
	Terrestrial + Emergent	-	2
Late	Terrestrial	1.003 ± 1.109	0
	Emergent	1.011 ± 1.063	0
	Water	0.986 ± 1.144	0
	Rice	0.987 ± 1.194	0
	Terrestrial + Emergent	-	2
	Emergent + Water	-	2
	Emergent + Rice	-	2
Post	Terrestrial	1.010 ± 1.106	0
	Emergent	1.006 ± 1.083	0
	Water	0.987 ± 1.225	0
	Rice	0.997 ± 1.164	0
	Terrestrial + Emergent	-	2
	Emergent + Water	-	2
	Emergent + Rice	-	2

Table 5. Model ΔAIC values for patch edge use analysis. Observed and associated random locations were combined and analyzed using a generalized linear mixed-effects model. Individual was always considered as a random intercept to account for multiple observations on a single individual. The uncorrected ΔAIC values are shown.

Model	*Description*	*ΔAIC*
Full Model	Location combination as fixed effect and random slope	0
Intermediate1	Location combination as only fixed effect	2
Intermediate2	Location combination as only random slope	4
Null model	No location combination, differences only from individual	24

Table 6. Odds ratio estimates for adult female Giant Gartersnake use of vegetation patches. Observed and random snake locations were recorded as edge or interior of patch. Edge was defined as being 0 – 3 m in width. The parameter estimates from a generalized linear mixed-effects model are shown (± 1 SE) along with the standard deviation of their associated random effect (Random SD). Estimates reflect the change in odds of that combination of locations occurring.

Observed	*Random*	*Estimate*	*Random SD*
Edge	Edge	1.94 ± 0.20	0.46
Edge	Interior	2.09 ± 0.21	0.52
Interior	Edge	0.59 ± 0.38	1.29
Interior	Interior	1.56 ± 0.31	1.23

Chapter 3

CONCLUSION

In our case study, we observed that Giant Gartersnake space-use was different between snakes living in an agricultural and a constructed wetland habitat. At Gilsizer Slough, home ranges of snakes in the agricultural habitat had smaller, less variable, and increased overlap between individuals when compared with snakes living in the nearby constructed wetland. Our results do not indicate a mechanism for these differences, so we could not answer whether high habitat quality or a high degree of fragmentation is the reason for the more restricted movements observed. However, extreme afternoon temperatures during the daytime and the selection by Giant Gartersnakes of emergent vegetation patch edges resulted in a reduction of suitable habitat. These results begin to describe limited habitat availability as a possible cause of restricted movements and increased space-use sharing among individuals (Ims et al. 1993; Verbeylen et al., 2009).

Our findings show that land managers may need to reconsider the classification of rice agriculture in habitat conservation plans for the Giant Gartersnake. Given the agricultural matrix within which conservation efforts must occur, rice agriculture cannot be discounted as habitat for the species, but connectivity within the subpopulations must be further investigated and addressed. Drainage management emphasizing minimal vegetation may inhibit dispersal into and establishment of newly constructed or restored wetland habitat. In order to maintain flow, California Department of Water Resources (CDWR) mechanically removes vegetation from within the drainages as often as funding and time allow.

Understanding movement related to vegetation cover was our goal in conducting an *in situ* experiment at Gilsizer Slough. We created 3 plots in the drainage with three randomly assigned vegetation treatments (no vegetation cover, intermediate vegetation cover, and dense vegetation cover) and intended to follow use of radio-tagged snakes within the plots. Ideally, we would have controlled the emergent vegetation (invasive primrose) from the beginning of its seasonal growth, but we were cooperating with CDWR which was experimenting with herbicide applications. Unfortunately, we were unable to collect data to test our hypotheses. We only had one Giant Gartersnake implanted within the experimental area despite intense trapping and search efforts. The vegetation manipulations were also uninformative because the control method, the herbicide (Aqua Neat, a glyphosate, Nufarm Americas, Inc.; Quest, a conditioning agent, Helena Chemical Co.), is most effective when primrose is flowering. This allowed the floating root-mass to become dense and was left even after the above-water portion of the primrose died back. The result was an incomplete removal of vegetation in the plots. The root-mass could still offer effective foraging areas by trapping prey and provide underwater refugia for snakes. Movements of even the single female Giant Gartersnake could not be related to incremental densities of primrose.

We also attempted to identify habitat use and movement in relation to environmental temperatures of microhabitats. Climate data from a nearby weather station was combined with temperature and vegetation composition data from our physical operative temperature models in a linear mixed-effects regression model. The intent was to predict snake operative environmental temperatures at the microhabitat scale, but after model selection procedures, our model predicted temperatures were related to macrohabitat, not microhabitat. This was a larger scale than was useful for habitat use models, and therefore was not included in those analyses.

Our case study brought attention to management issues, such as possible local fragmentation, habitat connectivity, and complex habitat structure. This re-emphasized the importance of emergent vegetation and water for the Giant Gartersnake during the active season. Although, this research does not confirm any mechanisms underlying Giant Gartersnake movement, we provide a basis for future research into the spatial ecology of this species. Studies focusing on prey distributions, survival, and connectivity between emergent vegetation patches would help explain the movements we observed during this study. Habitat loss is considered the largest constraint to the recovery of the Giant Gartersnake. With information on important aspects of habitat structure, management efforts could then be more efficient and effective in conserving and restoring habitat for the species.

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