

Original Research Article

Conservation reliance of a threatened snake on rice agriculture



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ABSTRACT

Conservation-reliant species require perpetual management by humans to persist. But do species that persist largely in human-dominated landscapes actually require conditions maintained by humans? Because most extant populations of giant gartersnakes (*Thamnophis gigas*) inhabit the highly modified rice agricultural regions of the Sacramento Valley, we sought to evaluate whether giant gartersnakes are indeed a conservation-reliant species dependent on maintenance of rice agriculture and its infrastructure for their continued existence. Specifically, we examined the extent to which giant gartersnakes use rice fields themselves, and whether survival of adult giant gartersnakes was influenced by the amount of rice grown near their home ranges and daily movements. We found that although giant gartersnakes only use rice fields minimally and then only between mid-June and early September, their survival was lower when less rice agriculture was available near the areas they inhabited. Survival was particularly low in early spring, when giant gartersnakes emerge from brumation but rice fields are not yet flooded. The incongruity between the phenology of rice growing and giant gartersnake foraging requirements suggests that although giant gartersnakes are reliant on the rice agroecosystem, rice agriculture is likely suboptimal habitat for giant gartersnakes. Giant gartersnakes' reliance on the rice agroecosystem challenges the notion of preservation-based conservation, but provides opportunities for win-win scenarios benefitting both rice farmers and giant gartersnakes. Our study highlights that in addition to land use, the timing of land management might be crucial for conservation-reliant species.

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1. Introduction

Conservation-reliant species require ongoing manipulation by humans to persist (Rohlf et al., 2014; Scott et al., 2010). These manipulations can focus on individuals and populations by maintenance of species wholly in captivity or captive rearing programs to augment small wild populations susceptible to extinction (Scott et al., 2005). Alternatively, manipulations to prevent extinction can focus on habitat management; when perpetual management is necessary to ensure that habitat for the species remains, the species also is considered conservation reliant (Scott et al., 2005). This latter form of

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conservation reliance is particularly important because the primary threat to many rare species is habitat loss (Böhm et al., 2013).

The loss of wetland habitats in the Central Valley of California, USA, has been severe. During the 20th Century nearly 95% of these wetlands were lost as most rivers draining into the Central Valley were dammed for irrigation, flood control, or hydroelectric power (Frayer et al., 1989; Garone, 2011). The loss of wetlands resulted in declines of many wetland-dependent wildlife, including waterfowl (Garone, 2011), amphibians (Fisher and Shaffer, 1996), and giant gartersnakes (*Thamnophis gigas*). Giant gartersnakes have been nearly extirpated from the southern two-thirds of their range, and most extant populations in the northern part of their range (the Sacramento Valley) occur in just over 200,000 ha of rice agriculture and its supporting infrastructure of canals (Halstead et al., 2010; U.S. Fish and Wildlife Service, 2017), which provide active season surface water and emergent vegetation necessary for giant gartersnakes.

Because rice is a crop and a commodity, the amount and extent of rice varies in response to weather, markets, and decisions made by individual farmers. The recent drought in California underscored the fragile nature of this system. In 2015 alone, surface water availability was reduced by 2.8 billion m³ in the Sacramento Valley (Howitt et al., 2015), so most farmers without senior water rights were unable to grow rice due to curtailment of water allocations. Indeed, from 2013 to 2015, the area of planted rice in California, 95% of it in the Sacramento Valley, decreased by more than 58,000 ha, or 25% (California Department of Food and Agriculture, 2016). Exacerbating the water shortage itself, the average price for Sacramento Valley water was \$0.53 USD/m³, which allowed water rights holders to generate more revenue by selling water to other users than by growing rice, an annual crop that is easily fallowed (Howitt et al., 2015). Future climate change and water use scenarios highlight the high demand for water and stresses to California's water delivery system caused by increased temperatures and reduced snowpack (Cayan et al., 2008; Hayhoe et al., 2004). Although giant gartersnakes in the Sacramento Valley have persisted in this system for the past 50–100 years, many questions remain about how giant gartersnakes are affected by the rice agroecosystem. For example, do giant gartersnakes require that rice is cultivated in the surrounding landscape, or can they persist in canals regardless of surrounding land use? Understanding how the distribution of surface water in the Sacramento Valley, driven largely by changes in rice agricultural practices, will affect giant gartersnakes is the most pressing concern for the conservation of this species.

We sought to understand the degree to which giant gartersnakes are a conservation-reliant species dependent on rice agriculture. Because population growth rates are most sensitive to the survival of adult females (Rose et al., 2018a), we evaluated how adult giant gartersnake survival is affected by the amount of rice agriculture around their daily locations and in the landscape surrounding their home ranges. Rice agriculture is the dominant source of surface water required by giant gartersnakes, and because they cannot readily disperse across large distances we expected that reductions in the amount of rice cultivated near snakes would increase their risk of mortality, supporting the idea that giant gartersnakes are reliant on rice agriculture.

2. Methods

2.1. Study sites

We conducted our study at 11 sites on private rice farms in the Sacramento Valley, California, USA. Sites were located in the Colusa Basin (Colusa County, four sites; Yolo County, two sites), Butte Basin (Butte County, two sites) and Sutter Basin (Sutter County, three sites; Table 1), and were selected to provide representation of rice agricultural practices during drought throughout the Sacramento Valley. Site selection was restricted to locations that had known populations of giant gartersnakes and landowners willing to allow access for the study.

The Sacramento Valley has a Mediterranean climate, with hot, dry summers and mild, wet winters. Historically, winter rains and snowmelt from the Sierra Nevada to the east resulted in the overflow of river channels and vast expanses of

Table 1

Total area (ha) and area of crop types (ha) in the minimum convex polygon around all giant gartersnake (*Thamnophis gigas*) observations by site and year in the Sacramento Valley, California, 2014–16. N = number of radio-tagged snakes. Values in parentheses are the percent of the site in each category each year.

Site	N	Total Area	2014			2015			2016		
			Rice	Other Crops	Fallow	Rice	Other Crops	Fallow	Rice	Other Crops	Fallow
1	7	1183.8	946.2 (79.9)	8.9 (0.8)	196.5 (16.6)	1023.4 (86.4)	8.6 (0.7)	126.8 (10.7)	1139.9 (96.3)	1.5 (0.1)	13.4 (1.1)
2	6	2177.7	1405.5 (64.5)	504.1 (23.1)	134.5 (6.2)	1067.5 (49)	401.4 (18.4)	572.4 (26.3)	1478.4 (67.9)	446 (20.5)	123.7 (5.7)
3	8	1251.3	786.6 (62.9)	22.7 (1.8)	402.2 (32.1)	806 (64.4)	13.3 (1.1)	388.7 (31.1)	1167.1 (93.3)	3.1 (0.2)	34 (2.7)
4	3	178.4	108.8 (61)	0.5 (0.3)	66.8 (37.4)	120.4 (67.5)	2.2 (1.2)	52.7 (29.6)	172.7 (96.8)	0 (0)	3.8 (2.1)
5	2	346.2	149.6 (43.2)	0.5 (0.1)	196.3 (56.7)	87.9 (25.4)	60 (17.3)	200.1 (57.8)	248.9 (71.9)	68.1 (19.7)	29.3 (8.5)
6	1	96.0	0 (0)	0.1 (0.1)	94.1 (97.9)	0 (0)	0.1 (0.1)	94.1 (97.9)	92.4 (96.3)	0.1 (0.1)	1.3 (1.3)
7	5	452.2	266.9 (59)	5.2 (1.2)	180.3 (39.9)	385.3 (85.2)	7 (1.6)	60.4 (13.4)	357.8 (79.1)	0.5 (0.1)	94.4 (20.9)
8	9	191.4	185.8 (97.1)	0.9 (0.5)	3 (1.6)	184.1 (96.2)	3.2 (1.7)	4.5 (2.4)	115.8 (60.5)	55.2 (28.8)	17.6 (9.2)
9	4	364.5	342.2 (93.9)	3.7 (1)	11.2 (3.1)	224 (61.5)	4.8 (1.3)	127.5 (35)	343.2 (94.2)	0.2 (0)	12.8 (3.5)
10	6	3217.7	3077 (95.6)	21.9 (0.7)	91.7 (2.9)	2817.7 (87.6)	134.9 (4.2)	245.4 (7.6)	2782.2 (86.5)	170.4 (5.3)	234.8 (7.3)
11	7	1677.2	211 (12.6)	844.0 (50.3)	578.8 (34.5)	825.1 (49.2)	610 (36.4)	198.5 (11.8)	672.1 (40.1)	828.2 (49.4)	130.5 (7.8)

emergent wetland habitat throughout much of the Central Valley (Singer et al., 2008). These wetlands have largely disappeared with agricultural development following flood control and irrigation projects (Fraye et al., 1989; Garone, 2011). Our study primarily occurred in and around the canals used as a water supply and drain for surrounding agriculture. Agriculture around the canals was dominated by rice, although some of the sites were surrounded by fallowed rice fields (Table 1). Rarely, other crops including tomatoes, alfalfa, and sunflowers were grown in adjacent fields.

Rice is grown in the Sacramento Valley as a summer annual crop. Although some variation in rice cultural practices exist, most rice fields are prepared for planting between mid-March and early May, then flooded and aerially seeded. Most fields remain flooded for the growing season, and rice plants form an emergent canopy beginning approximately in mid-June (Fig. 1). Fields are drained in late August and September, and rice is harvested in October and early November. After harvest, fields are typically disked and flooded to decompose rice straw and provide habitat for overwintering waterfowl.

2.2. Field methods

We captured giant gartersnakes for radio telemetry by trapping with modified floating funnel traps (Casazza et al., 2000; Halstead et al., 2013) and opportunistically by hand. In 2014, we selected seven sites for trapping, and trapped at each site between 9 May and 31 August (Table 1). In 2015, we selected four additional sites and continued trapping at all sites selected in 2014 (except Site 4) between 20 April and 9 September (Table 1).

We trapped at each site until we obtained five individuals large enough for radio telemetry. We measured, individually marked (by passive integrated transponder [PIT] tag, unique brand [Winne et al., 2006], or both), and determined the sex of each captured individual with sexing probes. We released all individuals <200 g mass at their location of capture immediately after processing, and we retained individuals ≥ 200 g in cloth sacks in climate-controlled chambers and transported them to the U.S. Geological Survey Dixon Field Station for radio transmitter implantation. Because most giant gartersnakes greater than 200 g are female, our sample of tracked snakes was mostly female.

After 1–5 days in captivity, we transported individuals to the Sacramento Zoo for surgery by an experienced veterinarian (Dr. Ray Wack, DVM), who surgically implanted Holohil SI-2T radio transmitters (9 g; Holohil Systems Ltd., Carp, Ontario, Canada; <http://www.holohil.com/>) into the body cavity of the snakes using standard methods (Reinert and Cundall, 1982). After recovery from anesthesia, post-surgical snakes were returned to the Dixon Field Station to recover for 1–2 weeks, during which time they were administered analgesics and antibiotics as prescribed by the veterinarian. We released individuals at their location of capture after they completed their course of prescribed analgesics and antibiotics and ate normally. We did not locate released individuals for one week post-release to allow them to further heal and re-acclimate to their natural environment.

We attempted to locate all radio tagged snakes daily during the active season (April–September) following their release, although difficulty obtaining radio fixes on snakes sometimes resulted in skipped days. During the inactive season (October–March), we located snakes weekly. We used R-1000 telemetry receivers (Communication Specialists, Inc., Orange, California; <http://www.com-spec.com/>) and handheld three-element yagi antennas (Wildlife Materials, Inc., Carbondale, Illinois; <http://wildlifematerials.com/>) to detect transmitter signals and locate snakes. Upon locating a snake or identifying a small (usually <2 m²) area from which the signal was strongest, we collected information on the individual's location and behavior, as well as environmental variables. In particular, we recorded the individual's location to <5 m accuracy in Universal Transverse Mercator North American Datum of 1927 (UTM NAD27) coordinates with a handheld global positioning system (GPS; Model eTrex 10, Garmin Ltd., <http://www.garmin.com/>). We flagged snake locations to help distinguish small-scale



Fig. 1. Laser-leveled rice field typical of rice agriculture in the Sacramento Valley, California, USA. USGS photograph taken 3 June 2017, just after rice plants have emerged above the water's surface.

movements from GPS error. In addition to location, we recorded whether an individual had moved more than 1 m since the last time it had been located, distance to water, and habitat type (irrigation canal, rice field, wetland, or other).

2.3. Analytical methods

We used a hierarchical binomial model with a logit-link function to evaluate the probability that giant gartersnakes used rice fields. We modeled the probability of use as a quadratic function of date, with intercepts and slopes modeled hierarchically to allow individual variation in the probability the snake was found in a rice field and the timing of rice field use. We also used a random intercept for year to allow for variation in snake use of rice fields among years. We specified priors for this model to be uninformative, with normal(mean = 0, SD = 1.65) priors on mean intercepts and coefficients and half-Cauchy(scale = 1) priors on standard deviations (Gelman, 2006).

We modeled survival based on snake mortality times using survival analysis (Williams et al., 2002). Because the survival process unfolds in time, using survival models that account for the amount of time snakes are at risk of mortality offers a more nuanced and statistically powerful approach than examining simple binomial outcomes. Briefly, survival analysis examines survival as a continuous process observed at discrete intervals and is based on the concept of a hazard, or risk of mortality within a short time interval (Williams et al., 2002). In the case of our models, we used constant hazards that assumed the risk of mortality was equal each day across the entire study (constant hazard) or within seasons (piecewise constant hazard). The survival models we used further accommodated staggered entry (individuals entering the study on different days), interval censoring (uncertain day of death), and right truncation or censoring (unknown fate or survival until the end of the study). Because we wanted to account for seasonal differences in the baseline risk of mortality, but also wanted to evaluate predictor variables that varied seasonally (e.g., proportion of active rice fields within 100 m of daily snake locations), we used two different formulations of survival models. For both models, we used daily time steps and set the beginning of the study to 25 June 2014, when the first individuals were released with radio transmitters. We also formulated both models as shared frailty models with a site-level random effect that allowed snakes from the same sites to have similar risks of mortality based on their shared characteristics (e.g., exposure to unmeasured variables such as contaminants, closer relatedness within sites than between sites, etc.; Halstead et al., 2012). Priors for all parameters of both models were selected to be uninformative (Table 2).

The first model we analyzed was a piecewise constant hazard model that allowed different daily risks of mortality in each of three seasons: 1) emergence from brumation (the reptile equivalent of hibernation) until flood up of canals and rice fields (April–May), 2) the remainder of the rice growing season and giant gartersnake active season (June–September), and 3) brumation (October–March). Within each of these seasons, giant gartersnakes were assumed to have a constant daily risk of mortality. To this piecewise constant baseline hazard, we added individual giant gartersnake covariates that might affect survival, including sex, snout-vent length (SVL) at the beginning of the tracking period, and the maximum proportion of active rice fields within 500 m of each individual's annual minimum convex polygon (MCP) home range. We chose 500 m as a buffer around individual home ranges because it represented the median of the maximum daily movement distance across snakes, thus representing a buffer on the same scale as the distance an individual might be expected to have been exposed to conditions around its home range. We derived the maximum proportion of active rice fields in and near a snake's home range with a custom Geographical Information System (GIS) rice classification tool that classified active rice fields with 96.3% accuracy (85.7% sensitivity and 97.5% specificity; Reyes et al., 2017). The annual cycle for this covariate began with the beginning

Table 2

Description of survival model parameters and their priors. Distributions are parameterized as follows: normal(mean, standard deviation), uniform(lower limit, upper limit), half-Cauchy(scale), and t(location, scale, degrees of freedom).

Model	Symbol	Description	Prior distribution
Piecewise constant hazard	S_{ijkl}	Survival function	Deterministic node
	CH_{ijkl}	Cumulative hazard (risk of mortality)	Deterministic node
	UH_{ijkl}	Daily hazard (risk of mortality)	Deterministic node
	γ_l	Piecewise baseline (constant) log hazard, for $l = 1$ (rice growing season), $l = 2$ (brumation), and $l = 3$ (active season prior to flood-up)	uniform(-11,-4)
	η_k	Random site effect	normal(0, σ_{site})
	σ_{site}	Site standard deviation	half-Cauchy(1)
	β_{sex}	Ln(hazard ratio) for males (relative to females)	t(0,1,1)
	β_{size}	Ln(hazard ratio) for snout-vent length	t(0,1,1)
	β_{r500}	Ln(hazard ratio) for proportion active rice fields within a 500 m buffer of annual minimum convex polygon home range	t(0,1,1)
	Constant hazard	S_{ijk}	Survival function
CH_{ijk}		Cumulative hazard (risk of mortality)	Deterministic node
UH_{ijk}		Daily hazard (risk of mortality)	Deterministic node
γ_0		Baseline (constant) log hazard	uniform(-11,-4)
η_k		Random site effect	normal(0, σ_{site})
σ_{site}		Site standard deviation	half-Cauchy(1)
β_{rice}		Ln(hazard ratio) for mean proportion active rice fields within 100 m of individual's location	t(0,1,1)
β_{c_rice}		Ln(hazard ratio) for cumulative mean daily proportion active rice fields within 100 m of individual's locations	t(0,1,1)

of the active season in one year, and ended at the end of the emergence and pre-flood-up period the following year. This allowed the effects of the proportion of active rice fields in the snake's home range to carry over through brumation and emergence until rice fields were once again available as habitat. Because only large adult snakes can be monitored with radio telemetry, we expected little growth during the tracking period for each snake (Rose et al., 2018b), and assumed that SVL at the beginning of the tracking period was a reasonable estimate of size for individual snakes for the duration of study. Continuous covariates (SVL and proportion of active rice fields) were centered and standardized to mean = 0, SD = 1 prior to analysis. The survival function for this model was

$$S_{ijkl} = e^{-CH_{ijkl}},$$

where

$$CH_{ijkl} = \sum_{j=1}^T UH_{1-j,ijkl},$$

$$UH_{ijkl} = e^{(\gamma_0 + \beta_{sex} \times sex_i + \beta_{size} \times SVL_i + \beta_{r500} \times rice_{500m} + \eta_k)},$$

and

$$\eta_k \sim \text{normal}(0, \sigma_{site}).$$

η_k represents shared frailty as a random site effect on the baseline daily hazard (UH_{ijkl}), and the cumulative hazard (CH_{ijkl}) is the sum of the daily hazards during the monitoring period (Table 2). Subscripts i, j, k, l , and m reference individual snake, day, site, season, and year, respectively, and T is the maximum number of days a population was monitored.

The second model we evaluated was a constant hazard model, for which the baseline probability of mortality was the same for every day of the study, but for which we allowed temporal variation in the hazard using individual covariates that changed daily. The covariates we examined for this model were the daily mean proportion of active rice fields within 100 m of the individual snake's locations and the cumulative (running) mean daily proportion of active rice fields within 100 m of the individual snake's locations. We chose a 100 m buffer around the individual locations because it approximated the maximum of the median daily movement distances across snakes, thus representing the landscape within which an individual might be expected to move on a given day. The daily mean proportion of active rice fields was used to estimate acute effects of the amount of actively growing rice near the snake on the daily risk of mortality, and the cumulative daily mean proportion of active rice fields was used to estimate cumulative effects of the amount of actively growing rice near the snake on the risk of mortality. The daily mean proportion of active rice fields naturally dropped to zero after harvest. For the cumulative mean proportion of active rice fields, we repeated the last calculated value during the rice growing season through brumation until flood up the following year. Because mean proportion active rice fields and cumulative proportion active rice fields were correlated ($\rho = 0.56, P < 0.001$), we selected the most informative covariate on risk of mortality by fitting a full model that used an indicator variable to turn off one of the active rice field covariates when the other was on. We then based inference on the active rice field covariate with the strongest support. The survival function under the full model was estimated as

$$S_{ijk} = e^{-CH_{ijk}},$$

where

$$CH_{ijk} = \sum_{j=1}^T UH_{1-j,ijk}$$

and

$$UH_{ijk} = e^{(\gamma_0 + (1-\omega) \times \beta_{rice} \times rice_{ij} + \omega \times \beta_{c_rice} \times c_rice_{ij} + \eta_k)}.$$

$\omega = 0$ activates acute effects of active rice fields and $\omega = 1$ activates cumulative effects of active rice fields, $rice_{ij}$ is the proportion of active rice fields within 100 m of snake i on day j , and c_rice_{ij} is the running mean of the proportion of active rice fields within 100 m of snake i from day 1 to day j . As before, η_k represents shared frailty as a random site effect on the baseline hazard. Subscripts are the same as for the first model, and definitions of parameters and their prior specifications are listed in Table 2.

All models were analyzed using Markov chain Monte Carlo methods as implemented in JAGS 4.3.0 (Plummer, 2017), run from R 3.3.1 (R Development Core Team, 2016) using the package jagsUI (Kellner, 2016). Survival models were run on 5 chains of 20,000 iterations each, after a burn-in period of 2000 iterations. The binomial model for rice field use was run on 5 chains of

200,000 iterations each, after a burn-in period of 100,000 iterations, and thinned by a factor of 10. We assessed convergence visually with history plots and with the \hat{R} statistic (Gelman et al., 2004); no evidence of lack of convergence existed (maximum $\hat{R} < 1.05$). Unless otherwise indicated, we report the posterior median and 95% symmetrical credible interval.

3. Results

We tracked 58 snakes (54 females, 4 males) at a total of 11 sites from 2014 through 2016, for a total of 7813 telemetry observations (number of observations per snake = 5–296). The majority (74%) of snake observations were within irrigation canals, with 12% of observations in terrestrial habitats (>5 m from water), 2% in marshes, and 12% in rice fields. Of the observations in rice fields, 71% were in active rice fields, 8% were in fallowed rice fields, and 20% were in dry rice fields during the inactive season. The probability that an average radio-tracked giant gartersnake used rice fields was very low, except between early June and late September, peaking at 0.11 (95% credible interval = 0.024–0.61) in early August (Fig. 2).

Of the 58 monitored snakes, 28 died, 5 were censored (not observed to die during the study) for unknown reasons (lost signal because of battery failure, movement beyond receiver range, etc.), and 25 were censored because we removed the transmitter and released the snake alive. Visual comparisons of model-based survival curves with Kaplan-Meier curves indicated no evidence for lack of model fit.

Based on the seasonal survival model, giant gartersnakes were at greatest risk of mortality as they emerged from brumation (Fig. 3). The median daily risk of mortality during emergence was 0.0053 (95% credible interval = 0.0024–0.010), whereas the daily risk of mortality during the active season and brumation were 0.0011 (0.0005–0.0023) and 0.0008 (0.0003–0.0015), respectively. Size had little or no effect on giant gartersnake survival (hazard ratio = 1.0 [0.64–1.6]), male risk of mortality was 0.46 (0.046–1.6) times that of females, and for every 23% absolute increase (1 SD) in the proportion of a snake's annual home range containing active rice fields, the risk of mortality was 0.51 (0.31–0.84) times as high (Fig. 4). Mean annual survival of adult female giant gartersnakes in our study with an average amount of rice production within 500 m of their home range (64%) was 0.54 (0.37–0.70). Annual estimated survival of adult giant gartersnakes with 18% active rice fields within 500 m of their annual home range (5th percentile) was 0.085 (0.0009–0.46), whereas annual estimated survival of snakes with 86% active rice fields in and near their home range (95th percentile) was 0.73 (0.53–0.87; Fig. 3).

Results of the constant survival model with temporal covariates were similar to those of the seasonal survival model. A cumulative effect of the proportion of active rice fields within 100 m of a giant gartersnake's location was 2.8 times more likely to be chosen by the model than acute effects of the amount of active rice fields, so we base further inference on the cumulative effects of active rice fields. The daily risk of mortality when a snake had a constant cumulative mean of 22% active rice fields within 100 m of its location (overall mean cumulative percent active rice fields across snakes) was 0.0013 (0.0008–0.0021), and the daily risk of mortality was 0.61 (0.38–0.94) times as high with a 17% absolute increase (1 SD) in active rice field cover within 100 m of the location (Fig. 5). Thus, annual estimated survival of a snake with a constant cumulative mean of 1% active rice fields within 100 m of its locations (10th percentile) was 0.40 (0.20–0.62), whereas annual estimated survival of a snake with a constant cumulative mean of 57% active rice fields within 100 m of its locations (95th

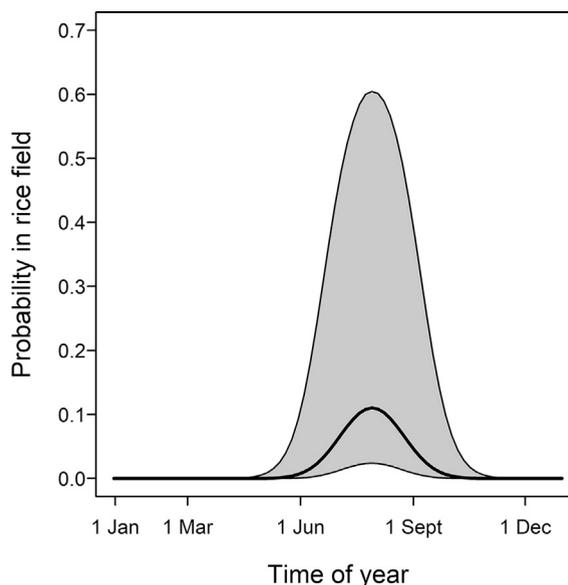


Fig. 2. Probability that an average adult giant gartersnake (*Thamnophis gigas*) is located within a rice field based on time of year. The bold line represents the posterior median; the shaded area represents the 95% credible interval.

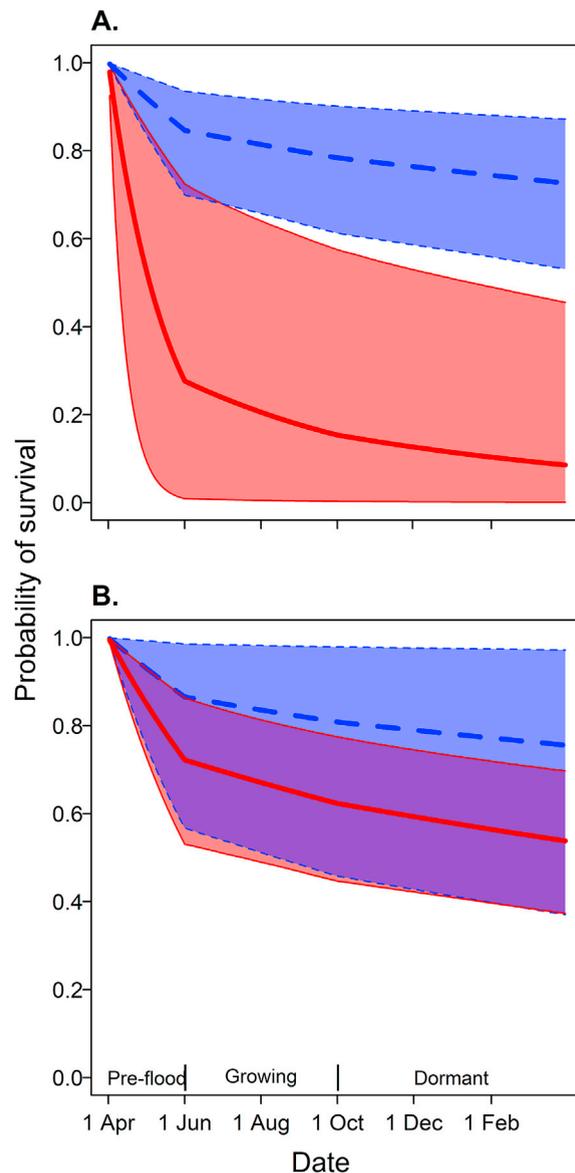


Fig. 3. Survival curves for adult giant gartersnakes (*Thamnophis gigas*) with A. 86% active rice fields within 500 m of their annual home range (95th percentile; blue area and dashed lines) or 18% active rice fields within 500 m of their annual home range (5th percentile; red area and solid lines), and for B. female (red area and solid lines) and male (blue area and dashed lines) giant gartersnakes based on the seasonal hazard model. Seasons along the x-axis in B. are relative to the rice agricultural practices in the Sacramento Valley, California, and approximately correspond to emergence and mating, the remainder of the active season, and brumation of giant gartersnakes. Bold lines indicate posterior medians; shaded areas and light lines indicate 95% credible intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

percentile) was 0.83 (0.60–0.95). At an average value of rice cover within 100 m of its locations (22%), annual adult giant gartersnake survival was 0.61 (0.46–0.74).

4. Discussion

Adult giant gartersnake survival was positively related to the amount of active rice agriculture surrounding the snake. The risk of mortality was lowest for snakes with the most rice growing in and near their home ranges, and those whose daily locations were near greater concentrations of rice agriculture. The positive effect of rice agriculture on giant gartersnake survival likely acts through an accumulation of conditions beneficial to the snakes, rather than immediate mortality when snakes do not have rice agriculture available to them. Interestingly, these benefits accrue even though many individual snakes were never observed in the rice fields themselves (Reyes et al., 2017), and those that were found in rice fields typically entered

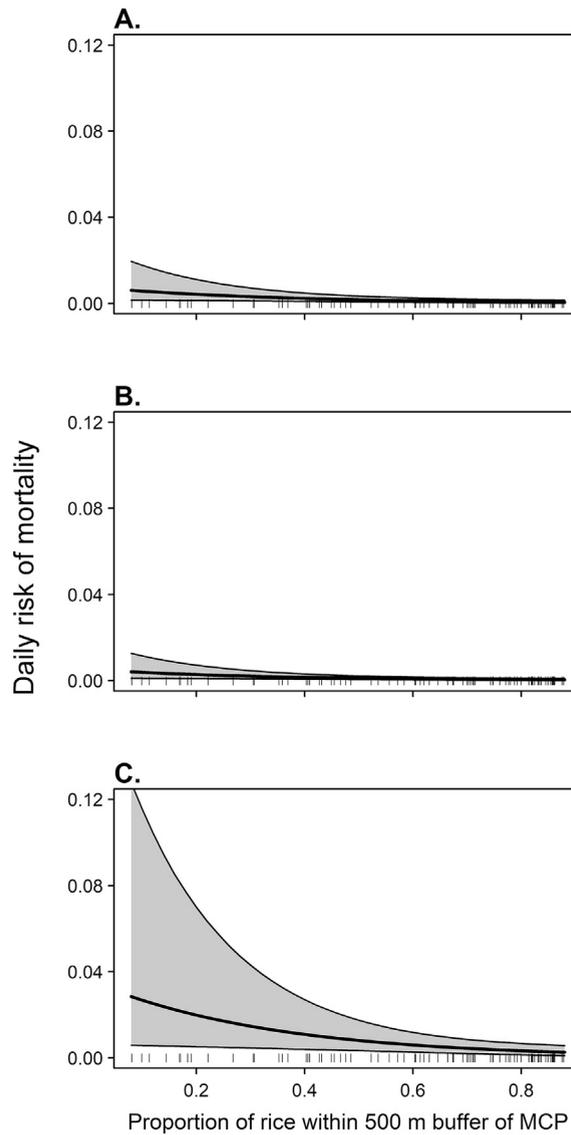


Fig. 4. Daily risk of mortality of giant gartersnakes (*Thamnophis gigas*) during A. the active season, B. brumation, and C. emergence and mating based on the proportion of active rice fields within 500 m of the individual's minimum convex polygon (MCP) home range. Bold lines represent posterior medians; gray shaded areas and light lines represent 95% credible intervals. Dashes along the x-axis indicate observed values.

them only when they were inundated and had emergent rice plants between mid-June and mid-September. Therefore, rice agriculture likely benefits snakes in adjacent canals by providing nutritional subsidies to prey species (i.e., allochthonous inputs of productivity from rice fields to canals; Polis et al., 1997), dispersing predators over a greater area, or both. Given that most extant giant gartersnake populations are partially or wholly dependent on the 200,000 + ha rice agroecosystem and nearly all giant gartersnake populations depend on human-mediated water deliveries for their persistence, giant gartersnakes are a conservation-reliant species (Rohlf et al., 2014; Scott et al., 2010).

Their current reliance on rice agriculture does not necessarily mean, however, that rice agriculture and its supporting infrastructure is optimal habitat for giant gartersnakes (Halstead et al., 2012; Wylie et al., 2010). Instead, giant gartersnakes have been able to persist in the marsh-like habitat that the rice agroecosystem provides, but not in other human-modified habitats within its former range. Nonetheless, giant gartersnake densities were lower in sites dominated by rice agriculture than in wetland sites (Wylie et al., 2010), and several aspects of rice agriculture could be detrimental to giant gartersnakes. Giant gartersnake survival was higher in two-dimensional habitats than in linear habitats (Halstead et al., 2012), but giant gartersnakes inhabiting rice agriculture are confined to linear canals for approximately half of the active season (April – mid-June and September; Fig. 1). In addition to increased risk of mortality in canals (Halstead et al., 2012), in this study we observed several snakes overwintering in fallowed fields, where they were at risk of injury or mortality during spring field

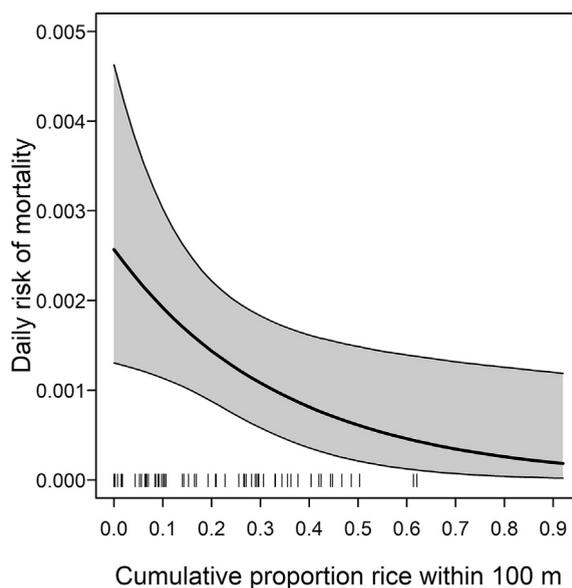


Fig. 5. Daily risk of mortality of giant gartersnakes (*Thamnophis gigas*) based on the cumulative mean proportion of active rice fields within 100 m of the individual's locations. The bold line represents the posterior median; the gray shaded area and light lines represent the 95% credible interval. Dashes along the x-axis indicate overall mean observed values for individual snakes.

preparation. One of these snakes was injured and removed from the study to receive treatment, and another was removed from a field as it was being disked and its survival data censored at the time of intervention. In addition to field treatments, two giant gartersnakes were separately found dead in a pump used to circulate irrigation water at one site. Whether the pump caused mortality or nearby carcasses were pulled into the pump cannot be ascertained, but we think the former cause is more likely. The cause of death could not be determined for most snakes because it was impossible to distinguish partial predation from scavenging and most intact individuals had multiple signs of disease (abscesses, parasites, tumors, poor condition, etc.) among which the primary contributor to death was unknown.

Agrochemicals also pose a potential threat to giant gartersnakes and their aquatic vertebrate prey. Frogs are sensitive to many pesticides (Sparling et al., 2015, 2001; Sparling and Fellers, 2007, 2009) and are important prey for giant gartersnakes (Ersan, 2015). Although taxonomically and ecologically similar snakes (viperine snake, *Natrix maura*) inhabiting a rice agroecosystem in Spain contained organochlorine pesticides (Santos et al., 1999), the effects of these and other agrochemicals on snakes are largely unknown. Perhaps because of agrochemicals, reduced prey availability, and other sources of habitat degradation, from 1995 to 2008 viperine snakes declined in rice fields but appeared to remain common in remnant wetlands (Santos and Llorente, 2009), suggesting that some aspect of the rice agroecosystem had changed to the detriment of the snakes.

Perhaps the most important aspect of the suitability of the rice agroecosystem for giant gartersnakes is the seasonal availability of aquatic habitat. Giant gartersnake survival was lowest in spring as snakes emerge from brumation and males search for mates. Mate-searching behavior did not appear to be related to increased risk of mortality in large adult males, however, because they trended toward having higher survival than females. Instead, increased risk of mortality in spring is likely related to nutritional stress as snakes emerge from brumation in late March and April. During this time, rice farmers typically prepare their fields for planting, and the rice fields and surrounding canals are dry. Giant gartersnakes forage almost exclusively on aquatic or semi-aquatic prey (Ersan, 2015), so they are exposed to a poor foraging environment until the canals and rice fields are flooded. Those snakes that emerge from brumation in a poor nutritional state are likely at high risk of starvation or other sources of mortality as they search for scarce prey. The timing of rice field flooding in mid-late May and emergence of rice plants in June is in contrast to the historical pattern of Central Valley marshes filling with winter rains and spring floods from large rivers overflowing their banks (Fraye et al., 1989; Garone, 2011). Reconciling giant gartersnakes' need for food in the spring with the delivery of water for agricultural purposes might reduce the risk of mortality in spring and provide benefits to snake populations.

Although giant gartersnakes persist in rice agriculture and opportunities exist to manage the rice agroecosystem to further benefit snakes, giant gartersnakes' reliance on rice agriculture presents challenges outside the normal scope of conservation actions. In particular, rice is an agricultural commodity and therefore subject to farmers' decisions about which crops to grow, particularly in response to market conditions. Perhaps more problematic than cropping decisions is the fluctuating supply and high demand for water in California. Increased temperatures in the 21st century will result in reduced snowpack and greater reliance on water storage (Cayan et al., 2008; Hayhoe et al., 2004) even if precipitation remains constant. The reduction in snowpack will further limit water supply, and because rice is an annual crop using surface water, this source is

often targeted to supply water for perennial crops like orchards as well as industrial and residential uses. Indeed, the impetus for this study was curtailment in water allocations to farmers and increased demand for water transfers during California's historic 2012–2016 drought. Our results suggest that if the amount of rice decreases, adult giant gartersnake survival and therefore population growth rates also will decrease (Rose et al., 2018a) unless alternative aquatic habitat is available to the snakes (Santos and Llorente, 2009). In the Sacramento Valley, the water delivery system used for agriculture maintains these alternative aquatic habitats; thus, giant gartersnakes are wholly reliant on human intervention to sustain survival probabilities compatible with population persistence.

Annualized survival probabilities of adult giant gartersnakes in our study are similar to other giant gartersnake survival studies and other natricine snakes. A similar telemetry study of giant gartersnakes found mean adult female survival probabilities to be 0.61 (95% credible interval = 0.41–0.79) in aquatic habitats, and higher in terrestrial habitats (Halstead et al., 2012). Survival estimates from capture-mark-recapture (CMR) studies of giant gartersnakes were approximately 0.51 (0.33–0.68; for snakes approximately 800 mm SVL based on Fig. 2) for giant gartersnakes throughout the Sacramento Valley (Rose et al., 2018c), 0.62 (0.37–0.82) for adult female giant gartersnakes in the American Basin (Hansen et al., 2015), and 0.73 (0.54–0.87) for the largest giant gartersnakes in the Natomas Basin (Hansen et al., 2015). The similarity of capture-mark-recapture estimates with radio telemetry estimates of adult giant gartersnake survival indicates that any bias caused by the potential for negative effects of radio transmitters on giant gartersnake survival are likely small. These telemetry- and CMR-based annual survival estimates are within the range reported for other natricine snakes (0.23–0.92; King et al., 2018), but they are perhaps lower than one might expect given the frequent positive relationship of natricine survival with size within species (King et al., 2018) and the large size of giant gartersnakes relative to all congeners and many other natricines. Rather than survival continuing to increase indefinitely with size, the survival ceiling model of Rose et al. (2018c) for giant gartersnakes was supported by the lack of a size effect on survival in our sample of large adult snakes. Far stronger than the effect of size in adult snakes was the positive effect of the amount of rice agriculture near snakes on their survival.

Although inhabiting the rice agroecosystem presents several risks to giant gartersnakes, they rely on the habitat and prey afforded by rice agriculture. Given the dominance of rice agriculture in the Sacramento Valley, it is difficult to imagine any contemporary land use compatible with giant gartersnake ecology that would approach the overall value of rice agriculture to giant gartersnakes. Reducing the amount of rice agriculture on the landscape decreases adult giant gartersnake survival, and removing it entirely would likely result in population declines and extirpation (Halstead et al., 2010). Although they are reliant on rice agriculture in the contemporary landscape, the rice agroecosystem is likely suboptimal habitat for giant gartersnakes, presenting sources of mortality not present in the historical landscape. Nonetheless, opportunities exist for improving the rice agricultural system for snakes by reducing the use of agrochemicals and increasing the duration of water and therefore prey availability during the giant gartersnake active season, especially during spring emergence. The reliance of species on agriculture challenges our notion of habitat management for rare species, but provides opportunities for win-win scenarios benefitting both farmers and species conservation.

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