Northern Mexican Gartersnake Demographics and Movement Ecology

Javan M. Bauder[1] Anthony Pawlicki[2], and Matt Goode[2]

1 U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit

2 University of Arizona

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For additional copies or information, contact:

Javan Bauder
U.S. Geological Survey
Arizona Cooperative Fish and Wildlife Research Unit
University of Arizona
Tucson, AZ 85721
mail: jbauder@usgs.gov

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Final Report for Task Order 23-3

Prepared by:

Javan M. Bauder[1], Anthony Pawlicki[2], and Matt Goode[2]

[1] U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, AZ
[2] School of Environment and Natural Resources, University of Arizona, Tucson, AZ

Photo credit: Anthony Pawlicki

Abstract

The northern Mexican gartersnake (*Thamnophis eques*; hereafter NMGS) is a federally threatened species occurring in riparian areas in central and southeast Arizona and west-central New Mexico. While previous studies have examined the ecology of this species in central Arizona, less is known about NMGS ecology in grassland landscapes of southeast Arizona. This project continues a long-term mark-recapture study of NMGS in the upper Santa Cruz River in the San Rafael Valley of southeast Arizona. We analyzed mark-recapture data collected by Arizona Game and Fish Department from 2008–2019 and included data we collected during 2022 and 2023. We also studied NMGS movement ecology using a combination of externally attached GPS transmitters and surgically implanted VHF transmitters. We had 517 NMGS captures over 26 survey sessions across the entire study, 186 of which were captures of previously marked snakes. Most of our captures were females and evidence of a statistically significant female-biased sex ratio was present on three survey sessions. Trapping success was generally highest June-September and catch-per-unit-effort (CPUE) was strongly correlated with the number of individuals captured. We used mark-recapture data from 288 individuals to estimate annual apparent survival and session-specific recapture probabilities. Annual apparent survival was higher for females (0.72, 95% highest posterior density intervals [HPDI] = 0.63–0.81) than for males (0.58, 95% HPDI = 0.44–0.72). Session-specific recapture probabilities were similar for males and females and were highly correlated with CPUE. During 2023, we monitored the movements of 13 adult females using GPS transmitters, two adult males using VHF transmitters, and one adult female using a GPS transmitter followed by a VHF transmitter. GPS transmitters were deployed from 7-18 days at a time as limited by battery life. After filtering out low-quality GPS locations, we obtained a total of 1,688 hourly GPS locations. Mean and maximum distances moved per hour ranged from 5.54–10.92 m and 15.24–135.71 m, respectively, across GPS transmitter attachment periods. Space use estimates from 100% minimum convex polygons ranged from 0.04–1.16 ha across GPS transmitter attachment periods. All documented NMGS movements during 2023 were relatively close (< 100 m) to the Santa Cruz River. These results continue to build upon our knowledge of NMGS ecology and suggest the continued presence of a relatively robust population within the upper Santa Cruz River.

Introduction

The northern Mexican gartersnake (*Thamnophis eques*; hereafter NMGS), a federally threatened species, occurs along riparian areas in central and southeast Arizona and west-central New Mexico. This species has undergone range-wide declines and these declines have been attributed to the loss and degradation of riparian and wetlands, loss of native prey species, and negative effects of nonnative fish and American bullfrogs (*Lithobates catesbeianus*) (Rosen and Schwalbe 1988, U. S. Fish and Wildlife Service 2014, Jones et al. 2020) although the impacts of these factors, particularly nonnative species, has yet to be quantitatively assessed. Most information on NMGS ecology comes from studies in central Arizona. For example, Emmons (2017) conducted a radio telemetry study of NMGS along the middle Verde River in north-central Arizona (Yavapai County, elevation = 959-1010 m) and Myrand (2019) conducted a radio telemetry study of NMGS along Tonto Creek upstream of Roosevelt Lake (Gila County, elevation = 670 m). These studies have provided information on NMGS population structure and natural history (Emmons and Nowak 2016a; b, Nowak et al. 2019). Boyarski et al. (2015) and Sprague and Bateman (2018) also used radio telemetry to study NMGS at the Arizona Game and Fish Department (AGFD) Bubbling Ponds Hatchery Complex (BPFH) near Oak Creek (Yavapai County, elevation = 1052-1180 m). These studies have provided valuable information on NMGS space use, movement patterns, and habitat selection. Additionally, information on NMGS population structure and demographics in central Arizona has come from mark-recapture studies at BPFH (Boyarski et al. 2019).

In contrast to central Arizona, less information is available on NMGS ecology from grassland landscapes in southeast Arizona. Arizona Game and Fish Department has been conducting mark-recapture surveys for NMGS in the upper Santa Cruz River in the San Rafael Valley since 2008 (AGFD, unpublished data). It is thought that the upper Santa Cruz River supports one of the largest NMGS populations in Arizona but this assessment has not been quantified. This landscape differs markedly from landscapes in central Arizona where NMGS studies occurred. The NMGS population at the upper Santa Cruz River occurs at a higher elevation (approximately 1440 m) and is situated in the middle of a broad expanse of Glains Grassland (Brown 1994). Numerous isolated stock tanks and ciénegas are present in the San Rafael Valley within approximately 10 km of the river and NMGS are occasionally observed in these waters. The upper Santa Cruz River contains large populations of nonnative fish and bullfrogs. It is therefore important to understand the population structure and demographics of NMGS in the upper Santa Cruz River to further evaluate the structure and status of this population.

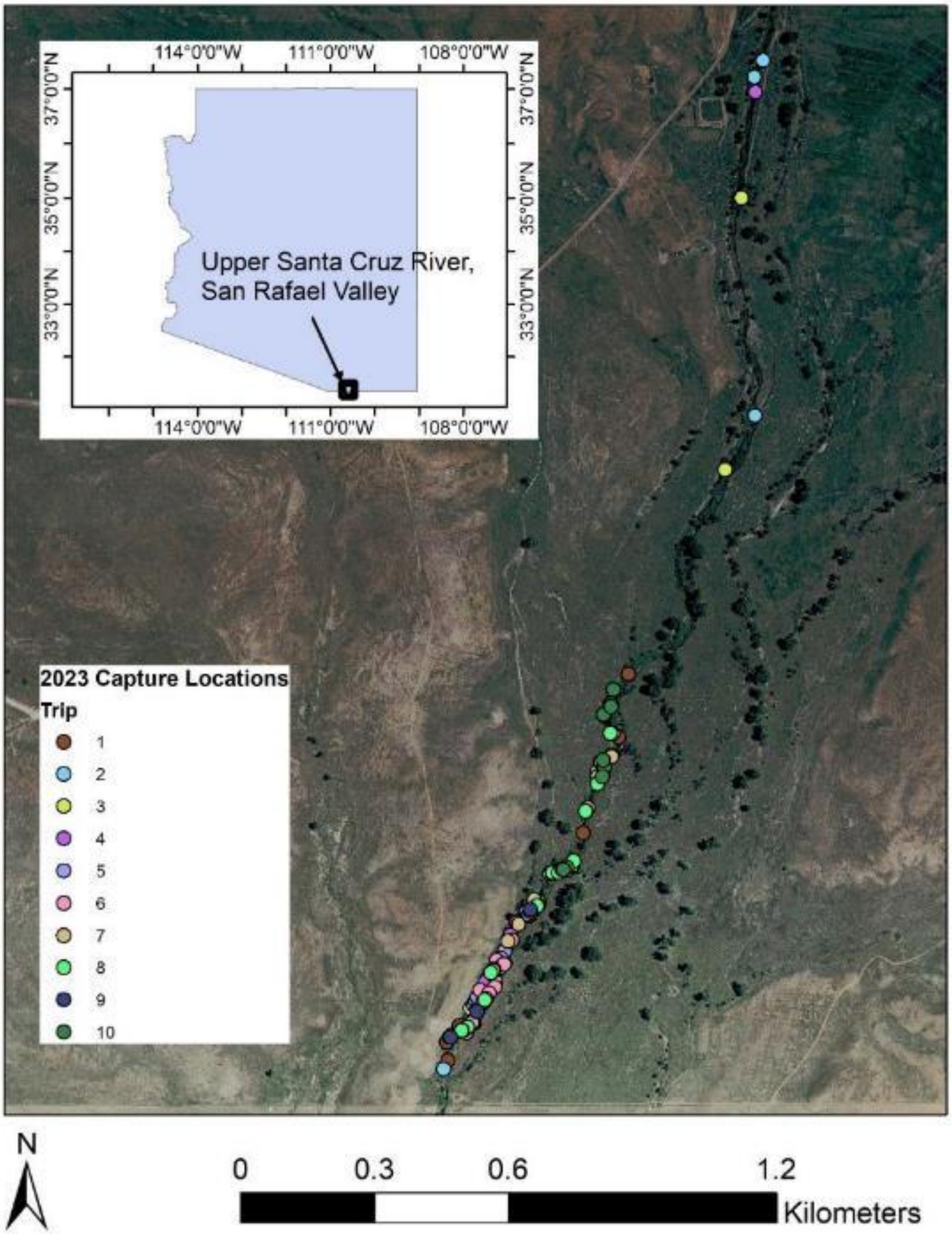
While NMGS are relatively easy to detect at the upper Santa Cruz River, observations at the nearby stock tanks and cienegas are infrequent and rare. The reasons for this disparity are unclear and could reflect differences in sampling effort and the ephemeral nature of these isolated water bodies. It is unclear if NMGS observations at stock tanks and cienegas represent sporadic long-distance movements or are indicative of a broad scale metapopulation. Therefore, it is important to also evaluate the spatial ecology of NMGS in the San Rafael Valley. However, the spatial extent of this system and the infrequency of NMGS observations outside of the Santa Cruz River pose many logistical challenges for the use of mark-recapture or traditional very high frequency (VHF) telemetry for monitoring NMGS movements with handheld devices. During 2022, we tested the application of a new technology, Lotek's PinPoint Beacons, transmitters that use GPS technology to record locations and VHF for real-time monitoring and retrieval, to evaluate the movement patterns of NMGS. We found that these transmitters were capable of recording hourly GPS locations on NMGS, although their short battery life limited their applicability (M. Goode, unpublished data). To our knowledge, this study represents the first application of these transmitters on a semi-aquatic snake, and is among the first applications for snakes, in general.

We had two primary goals in this study. The first was to provide empirical estimates of population demographic parameters by continuing ongoing mark-recapture surveys for NMGS in the upper Santa Cruz River within the San Rafael Valley that were begun by AGFD in 2008. The second goal was to use Lotek's PinPoint GPS/VHF beacons to monitor and document the movement patterns of NMGS between the upper Santa Cruz River to the surrounding uplands.

Methods

Study Area. We conducted this study along a 2.7 km stretch of the upper Santa Cruz River in the San Rafael Valley (31.335N, 110.597W WGS 84, 1403 m elev; Figure 1). Southwestern riparian vegetation, dominated by Gooding willows (*Salix gooddingii*) and Fremont's cottonwoods (*Populus fremontii*), is present along the river, and adjacent uplands are dominated by a Plains Grassland community (Brown 1994). The river includes a mixture of deep slow-moving pools and shallower stretches with visible current. Semi-aquatic and aquatic vegetation is abundant along the river, including bulrush (*Scirpus* spp.) and cattail (*Typha* spp.). Nonnative American bullfrogs and fish, including green sunfish (*Lepomis cyanellus*), mosquitofish (*Gambusia affinis*), largemouth bass (*Micropterus salmoides*), and black bullhead (*Ameiurus melas*), are present in the river, as well as native longfin dace (*Agosia chrysogaster*; AGFD, unpublished data). Because the study area is located in the San Rafael State Natural Area, cattle grazing along the river is generally prohibited; however, small numbers of cattle have grazed within the site under certain circumstances, such as permission to graze in the area after fire affected neighboring ranches.

Figure 1. Map of northern Mexican gartersnake study area in the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, and the location of all gartersnake captures during 2023 by trapping session (i.e., trip).



Mark-Recapture Surveys. Mark-recapture surveys (hereafter trapping sessions) for NMGS on the upper Santa Cruz River were conducted during 2008, 2012–2016, 2018–2019, and 2022–2023. Sessions conducted prior to 2022 were conducted by AGFD. Sessions were conducted by placing 34-150 (mean maximum number of traps per survey = 94) Gee minnow traps with ⅛” mesh for 3-10 nights (mean = 6.5 nights) per survey. Traps were generally placed parallel to the shoreline, submerging no more than three-quarters of the trap to allow captured snakes to breathe. We placed an approximately 20-cm piece of foam tubing in each trap to maintain trap buoyancy and secured traps to stakes driven into the stream bank. We checked traps at least twice per day, once in the morning and once in the afternoon. We did not bait traps but traps quickly self-baited with fish and bullfrogs (tadpoles and metamorphosed individuals). During the 2023 season, our traps were periodically raided at night by raccoons (*Procyon lotor)* with traps pulled up on the banks and the end funnels pulled open, presumably to access the trap contents. Beginning on 15 August 2023, we removed any fish and bullfrogs (i.e., “bait”) from all traps during the afternoon check and placed them in 10-gallon buckets with water. The next morning, we placed the bait back into each trap with a haphazard assignment of bait to traps.

During this study, traps were placed throughout the same approximately 2.7 km study reach although the number of traps and their placement varied from session to session depending on logistical support and the availability of sufficiently deep water. During 2023, we categorized the location of each trap to one of the following habitat categories during each session: pond <10m long, pond 10-20m long, pond >20m long, grassy narrow stream, marsh, off-channel pond, or dry active channel. Grassy narrow stream reaches had moving water while marshes did not. Off-channel pools were in the riverbed but were not connected to the main channel of the Santa Cruz River during low water periods. Habitat categorizations for a given site could change within sessions due to fluctuating water levels, particularly during the below-average 2023 late summer rainfall (i.e., monsoon; Adams and Comrie 1997).

We calculated the number of trap-hours for each trap, both for each session and for the entire field season, and for each habitat category. If the habitat category for a trap changed within a trap session, we determined the number of hours for each habitat category. If a trap was raided by a raccoon or another animal and was damaged to a point where NMGS could more easily escape (i.e., enlarging the trap opening), we did not include the hours between when the damaged trap was found and the previous trap check.

For each captured NMGS, we recorded its sex, mass, snout-vent length (SVL), tail length, and head width and length (2023 only). Length measurements were taken by gently stretching the gartersnake along a tape measure except during 2022 and 2023 when individuals were anesthetized using Isoflurane prior to taking weight and length measurements. We marked each gartersnake with SVL >245 mm with a subcutaneously injected passive integrated transponder (PIT) tag. During some years of the study, ventral scale clipping was also used to individually mark gartersnakes. During 2023, we began marking neonate gartersnakes with subcutaneously injected visual implant elastomer (VIE) (Major et al. 2020). We also noted the presence of any injuries (e.g., injured tails, scars), ova or semen, prey bolus, or regurgitated prey and we attempted to procure a fecal sample. Additionally, we collected a genetic sample from each individual by taking a scale clip or clipping the distal <5 mm of the tail and taking a blood sample on filter paper (Advantec, 55mm) from the open wound. We sealed wounds with a hand-held medical cauterizing unit and released all gartersnakes at their capture location. We stored tissue samples in 70% ethanol alcohol and froze blood samples. All samples were stored at the University of Arizona.

We calculated catch-per-unit-effort (CPUE) as both the number of trap-hours per snake capture and the number of snake captures per trap-hour. We tested if sex ratios differed significantly from 1:1 using chi-square goodness of fit tests or, when cell sizes were <5, Fisher's exact tests. We adopted a conservative approach to assigning sex such that if a given individual had different sexes within the database (e.g., recorded as a female one year and as a male several years later), we considered sex to be unknown ($n = 2$ snakes). We used linear mixed-effects models with random intercepts by snake ID to test for differences in SVL, tail length, head width, and head length between males and females using the 2023 capture data. We compared differences in CPUE across months using a Kruskal-Wallis test. We report mean sizes and standard errors using the expected values from our mixed-effects models. Unless otherwise noted all values reported are means ± one standard error.

Survival Analyses. We used a Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) to estimate annual apparent survival and recapture probabilities. We fit two versions of this model. The first model was to estimate annual apparent survival, so we pooled all captures and recaptures into 10 annual capture occasions. The second model was to examine finer-scale variation in recapture probability, so we considered each individual session (*n* = 26) as a unique capture occasion. In each model, we included sex as a fixed-effect covariate on apparent survival and recapture probability and modeled additional variation in recapture probability using random-effects of sampling occasion. Because capture occasions in both models were not evenly spaced, we incorporated the length of time between capture occasions to provide annual and 30-day apparent survival estimates, respectively.

We fit our models as Bayesian state-space models (Kery and Schaub 2012) using JAGS (v. 4.3.0, Plummer 2003) implemented using the package jagsUI (v. 1.5.1, Kellner 2019) (v. 1.5.1, Kellner 2021) in Program R (R Core Team 2021). We used uninformative priors Beta(1,1) for the intercept of survival probability and the overall mean recapture probability, Uniform(0,10) for the standard deviation of the random-effects and Gaussian(0,1.6) for the coefficient of effect of sex. For individuals of unknown sex, we randomly assigned a sex during each iteration based on the estimated sex ratio from the data with a Beta(1,1) prior. We ran 25,000 adaptive iterations followed by 25,000 burn-in iterations and then sampled the 10th posterior sample from another 25,000 iterations across three parallel chains. We report posterior means and 95% highest posterior density intervals (HPDI). We confirmed sufficient model convergence by examining trace plots and ensuring that all Gelman-Rubin statistics ($\hat{R}$) were ≤1.02 for all parameters (Brooks and Gelman 1998, Gelman and Hill 2006). We tested for a correlation between snakes captured per trap-hour and session-specific recapture probabilities using a Spearman's rank correlation.

Radio Telemetry. We used two types of radio transmitters to monitor NMGS movements during 2023. We affixed 4.8-gram dual GPS-VHF beacons (PinPoint VHF-75, Lotek, New Market, Ontario, Canada; hereafter GPS transmitters) to the dorsum of NMGS around the middle of the body using duct tape (Duck Brand; Wylie et al. 2011). We programmed each GPS beacon to record a GPS location every hour during a 24-hour period. We also surgically implanted 3.8- or 5-gram VHF transmitters (SB-2T, Holohil Systems Ltd., Carp, Ontario, Canada; hereafter VHF transmitters) in two males and one female, respectively, using the methods described by Weatherhead and Anderka (1984). We located all telemetered individuals approximately once per day during each trapping session using a VHF H-style antenna (Telonics, Model RA-23K) and receiver (Communication Specialists, Model R-100).

We tracked telemetered individuals once per day during a trapping session to maintain contact with telemetered individuals, evaluate the accuracy of the GPS transmitter locations, observe behaviors, and determine if the GPS transmitters were still attached. Each time we located a snake, we recorded the GPS location in UTMs using a hand-held Garmin GPS unit. We also recorded air temperature (°C) and relative humidity (%) at 1 cm and 1 m aboveground using a Kestrel 3000 Pocket Weather Meter. We also recorded habitat type and the behavior of the snake. When possible, we captured snakes to inspect the tape securing the GPS transmitter or the suture where the VHF transmitter was implanted. Finally, we weighed each snake after its capture. We attempted to capture each GPS-telemetered snake before the transmitter battery expired to attach a new GPS transmitter.

We downloaded GPS locations from GPS transmitters either directly upon recapturing a snake to replace or remove the GPS transmitter using the DLC-2 Lotek Comm, or remotely in the field using the Lotek Pinpoint Commander. We evaluated the quality of all GPS locations by using the number of satellites to which the unit was connected and the horizontal dilution of precision (HDOP). We only included locations where the unit had an HDOP ≤ 5, following a recommendation by support staff from Lotek (G. Jones, personal communication) and was connected to at least five satellites. We used these locations to calculate 100% minimum convex polygons (MCP) in QGIS version 3.36.0. We also calculated Euclidean distances between consecutive hourly locations during each snake's tracking period. We also summarized the time it took a GPS transmitter to acquire a GPS location as this can impact battery longevity.

Results

We used capture data from 26 survey sessions from 2008 through 2023 with sessions occurring from April through October across the study (Table 1). The trap-hours per session ranged from 2840 to 21983 (mean per session = 11485 ± 1027). During this time, we had a total of 517 captures of NMGS (mean = 20 ± 2.74): 331 captures of previously unmarked NMGS (mean = 13 ± 2.05) and 186 captures of previously marked NMGS (mean = 7 ± 1.26). Most NMGS that we captured were females (278 females and 164 males) and this ratio was significantly different from 1:1 ($\chi^2 = 29.40$, $P < 0.0001$). While sex ratios were generally female-biased during sessions, the sex ratio of captured NMGS was only significantly ($P < 0.05$) female-biased in three of 25 sessions where both sexes were captured (July 2018, July 2019, and August 2019;

Table 1; Figure 2). The vast majority of captures were adults (360) compared to subadults (72). The number of trap-hours per NMGS capture ranged from 105-3985 (mean = 1074 ± 209). There was some evidence that trapping success (i.e., snakes captured per trap-hour) varied by month with peaks during July, August, and September (Figure 3). There was also statistical evidence that trapping success differed among months ($\chi^2 = 11.45$, $P = 0.0754$; June-September data only).

Table 1. Summary of trapping effort (number of traps and total trap-hours) and captures of northern Mexican gartersnakes in the upper Santa Cruz River in the San Rafael Valley, Arizona, during 2008-2023 by trapping session. New Caps = captures of previously unmarked snakes; Re-Caps = captures of snakes marked during current or previous capture occasions; Total Caps = total number of captures; Sex = ration of female (F) to male (M) captures; Age = ratio of adult (A) to juvenile (J) captures; Trap Caps = number of captures made in traps; CPUE = trap-hours required to capture one snake/snakes captured per trap-hour. ** indicates P < 0.05 and * indicates P < 0.10.

Trip	Year	Start Date	End Date	No. Traps	Trap-Hours	New Caps.	Re-Caps.	Total Caps	Sex (F:M)	Age (A:J)	Trap Caps.	CPUE
T1	2008	14-Jul	22-Jul	102	19584	37	4	41	10:3	36	40	490/0.00204
T2	2008	11-Aug	19-Aug	102	18115	15	2	17	14:3	16	17	1066/0.00094
T3	2012	28-Aug	31-Aug	101	9019	24	5	29	19:10	25:1	29	311/0.00322
T4	2013	4-Sep	6-Sep	101	6615	11	5	16	9:7	13	15	441/0.00227
T5	2014	25-Aug	27-Aug	102	6732	10	5	15	10:4	13:2	14	481/0.00208
T6	2015	31-May	5-Jun	102	13668	24	6	30	19:11	28:1	27	506/0.00198
T7	2016	16-Apr	19-Apr	102	7344	6	1	7	4:3	5:1	6	1224/0.00082
T8	2016	29-May	3-Jun	102	12240	12	5	17	9:7	13:2	15	816/0.00123
T9	2018	16-Jul	19-Jul	77	5554	45	14	59	44:12**	19:12	53	105/0.00954
T10	2019	24-Jun	28-Jun	100	9600	1	2	3	2:1	3:0	3	3200/0.00031
T11	2019	22-Jul	25-Jul	116	8352	13	9	22	19:3**	13:5	21	398/0.00251
T12	2019	19-Aug	23-Aug	100	9600	16	15	31	21:8**	21:5	30	320/0.00313
T13	2019	19-Sep	23-Sep	101	9696	8	12	20	14:6*	17:0	20	485/0.00206
T14	2019	17-Oct	21-Oct	100	9600	8	9	17	3:12	17:0	16	600/0.00167
T15	2022	6-Jun	10-Jun	60/114	8112	5	0	5	2:3	1:0	5	1622/0.00062
T16	2022	4-Sep	11-Sep	50	8400	3	0	3	2:0	3:0	3	2800/0.00036
T17	2023	23-May	29-May	150	21375	6	2	8	4:4	7:0	8	2672/0.00037
T18	2023	6-Jun	12-Jun	67/156	19926	4	1	5	2:3	5:0	5	3985/0.00025
T19	2023	20-Jun	26-Jun	156	21983	4	4	8	4:4	6:1	8	2748/0.00036
T20	2023	4-Jul	13-Jul	50	9939	14	6	20	10:7	17:2	17	585/0.00171
T21	2023	18-Jul	27-Jul	50	10953	13	9	22	9:5	15:5	21	522/0.00192
T22	2023	1-Aug	9-Aug	50/90	16289	18	21	39	11:14	20:13	38	429/0.00233
T23	2023	15-Aug	24-Aug	50/90	15654	16	12	28	12:8	13:12	27	580/0.00172
T24	2023	29-Aug	7-Sep	36/50/54	10863	12	26	38	16:20	20:8	38	286/0.0035
T25	2023	15-Sep	18-Sep	40	2840	1	3	4	1:1	2:1	4	710/0.00141
T26	2023	23-Sep	1-Oct	34	6562	5	8	13	8:5	12:1	12	547/0.00183

Figure 2. The proportion of female northern Mexican gartersnakes captured by trapping session across months along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during 2008-2023. Error bars represent 95% confidence intervals estimated using binomial generalized linear models and the horizontal dashed line represents 0.50.

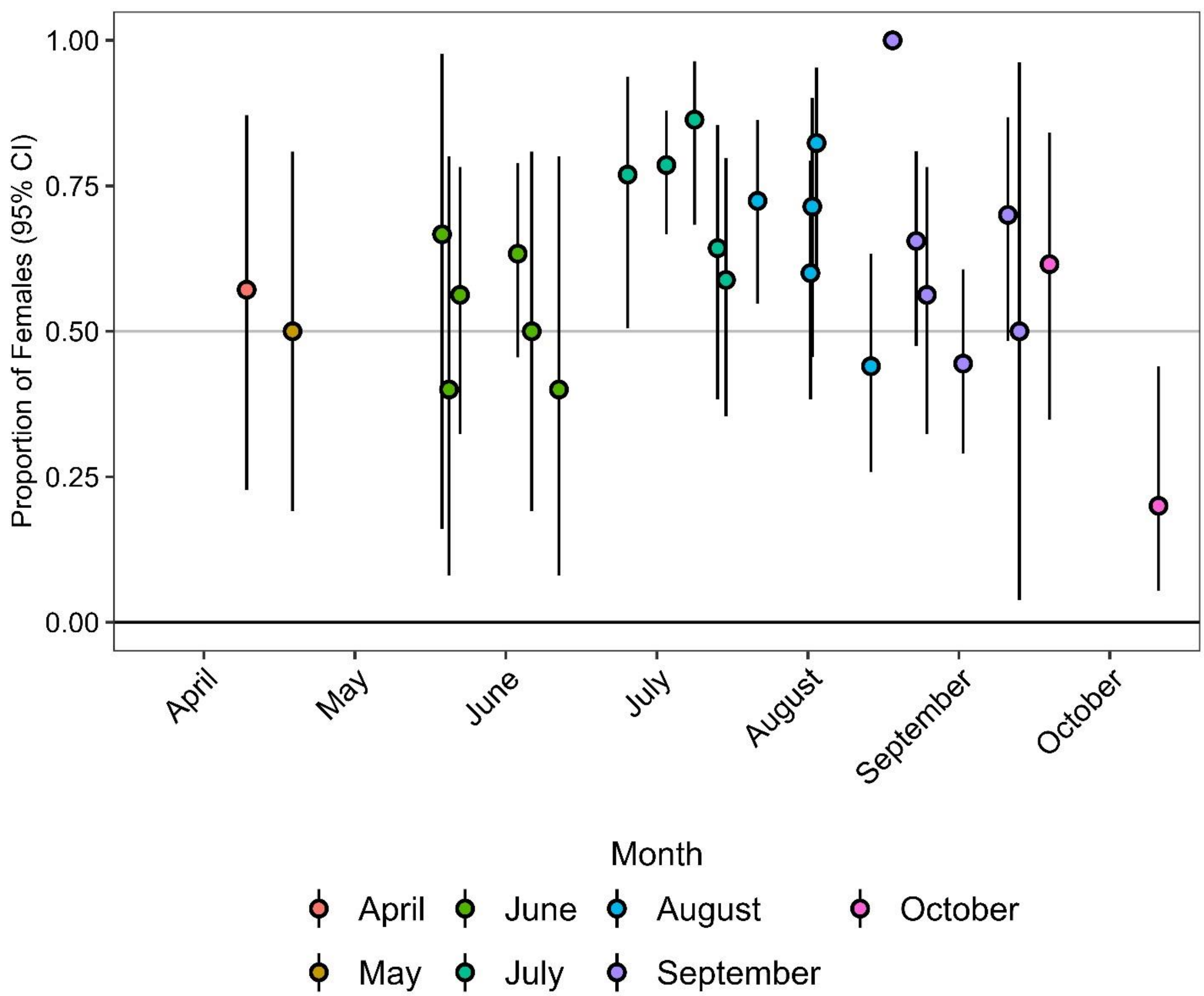
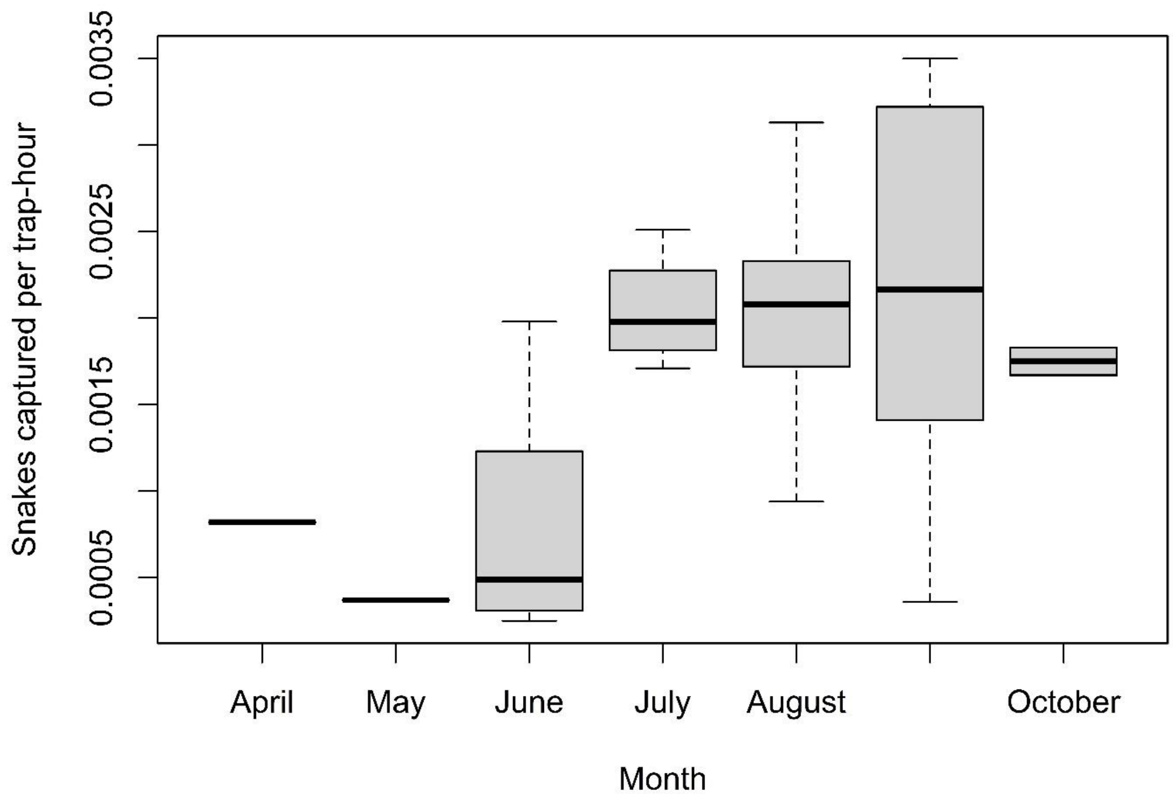


Figure 3. Northern Mexican gartersnakes captured per trap-hour by month in the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during 2008-2023. For visualization purposes, we excluded an outlier of 0.0095 snakes captured per trap-hour from July 2018.



2023 Mark-Recapture Results. During 2023, we conducted 10 trapping sessions between 23 May and 1 October (Table 1). During this time, we captured 84 unique NMGS that we marked using PIT-tags or VIE. Additionally, we captured 21 neonate NMGS that we did not mark. Of the 84 unique individuals, 11 were captured and marked prior to 2023. We had a total number of 194 NMGS captures during the field season, eight of which were hand captures and four of which were recaptured using telemetry. We recaptured 41 (49%) of the NMGS that we marked during 2023 at least once during 2023. The mean number of recaptures for all individuals was 1.09 ± 0.17 and 2.07 ± 0.22 recaptures when only using individuals that were recaptured. The number of recaptures ranged from 1-7.

Of the 84 unique marked individual NMGS, 61 were adults, 22 were neonates, and one was a juvenile. The ratio of adults to subadults (61:23) was significantly different from 1:1 (χ^2 = 17.19, $P < 0.0001$). We marked 34 male and 40 female NMGS for a sex ratio not significantly different from 50:50 (χ^2 = 0.45, P = 0.4855). Female NMGS were significantly larger than male NMGS in snout-vent length (β = -143.05, P = 0.0004; F: 619.31 ± 27.39 mm; M: 476.26 ± 29.71 mm), mass (β = -75.31, $P < 0.0001$; F: 146.93 ± 11.59 g; M: 71.62 ± 12.59 g), head width (β = -4.67, $P < 0.0001$; F: 17.09 ± 0.70 mm; M: 12.41 ± 0.76 mm), and head length (β = -7.19, $P <$ 0.0001; F: 30.68 ± 1.13; M: 23.49 ± 1.23 mm). We processed NMGS on 164 occasions (including recaptures). Of the 164 occasions, we felt the presence of at least one prey bolus on 149 occasions (90.85%), observed a fecal sample on 49 occasions (29.88%), and observed regurgitation 15 times (9.15%). Eleven of these 15 regurgitations consisted of bullfrog tadpoles, two of metamorphosed bullfrogs, two of mosquito fish, and two of unknown items. Two captured female NMGS were gravid (determined by palpation; one captured on 28 May and the other 17 July) with an estimated 13 and 9 ova, respectively. We documented semen present in four males captured between 9 July and 3 September.

We documented injuries on 31 (37%) individuals mostly in the form of injuries to the tail or part of the tail missing. Of 163 processing occasions where tail status was recorded, the tail was intact on 97 of those occasions, partially missing on 62 occasions, and fully missing on one occasion.

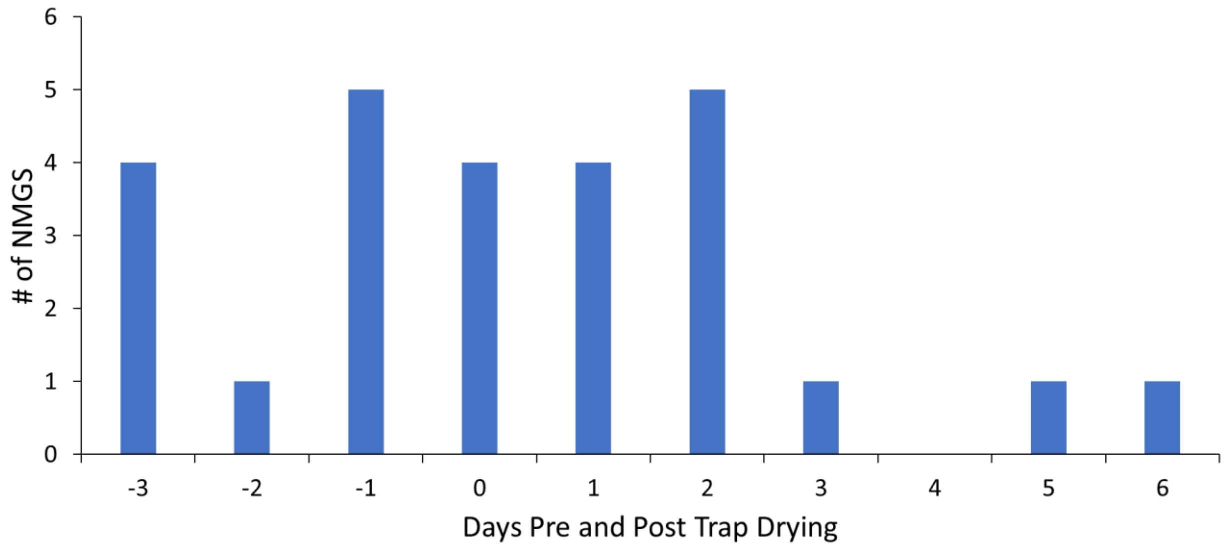
Our CPUE increased throughout the 2023 field season and was strongly correlated with number of individuals captured per session (r = 0.84). Our largest effort to catch one NMGS in a trap session was 3,985 hours per NMGS during early June while our lowest was 286 hours per NMGS during late August (Table 1). We caught more snakes during our afternoon checks (164) than we did during our morning (11) or midday checks (3; midday checks only occurred during the first session). Additionally, we saw success with traps that we randomly baited in the mornings after pulling bait during the afternoon check. We baited traps on 507 occasions and these traps captured one NMGS 53 times (10.45%) and two NMGS 7 times (1.38%). During the sessions that we baited traps, they contained 67 NMGS while non-baited traps had 47 NMGS (χ^2 = 3.51, P = 0.0610).

The CPUE for NMGS varied by habitat type. The lowest CPUE occurred in ponds 10-20 m long (3.665.63 trap hours per NMGS), ponds > 20m long (2,152.30 trap hours per NMGS), ponds <10m long (1,580.42 trap hours per NMGS), and marshes (1,028.65 trap hours per NMGS). Traps in dry active channels had the greatest CPUE (176.38 trap hours per NMGS), followed by grassy narrow streams (334.12 trap hours per NMGS) and off-channel ponds (382.32 trap hours per NMGS; Table 2). Most NMGS were caught within 1 day before the trap was totally dry to 2 days after the trap was totally dry (Figure 4).

Table 2. Trapping effort and trap captures of northern Mexican gartersnakes (NMGS) by habitat type for traps placed along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during 2023.

Habitat Type	Number of Traps	Total Number of Trap-Hours	Number of NMGS Captures	Trap Hours per NMGS Captured
Pond <10m long	32	4,741.25	3	1,580.42
Pond 10-20m long	47	7,331.25	2	3,665.63
Pond >20m long	304	47,350.5	22	2,152.30
Grassy Narrow Stream	100	14,701.25	44	334.12
Marsh	86	13,372.5	13	1,028.65
Off-Channel Pond	139	22,174.25	58	382.32
Dry Active Channel	41	4,938.75	28	176.38

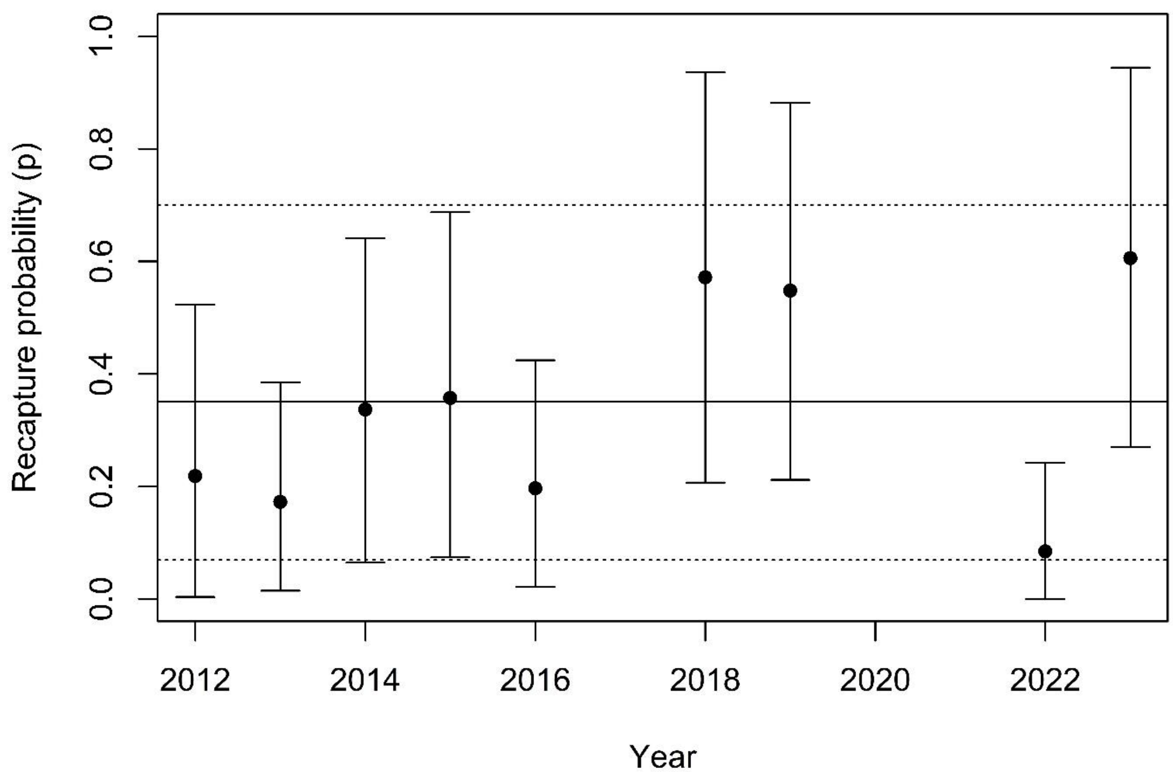
Figure 4. Number of northern Mexican gartersnakes (NMGS) that were caught each day, before (negative numbers) and after (positive numbers) the water at a trap had dried (i.e., no more standing water in or under the trap) for traps placed in the upper Santa Cruz River, San Rafael Valley, Arizona, USA, during 2023.



Survival Analyses. For mark-recapture analyses, we used data from 288 uniquely marked individuals including 159 females, 92 males, and 37 individuals of unknown sex. Of these 288 individuals, 36 were recaptured in at least one subsequent year (27 snakes recaptured in one subsequent year, eight snakes recaptured in two subsequent years, and one snake recaptured in three subsequent years).

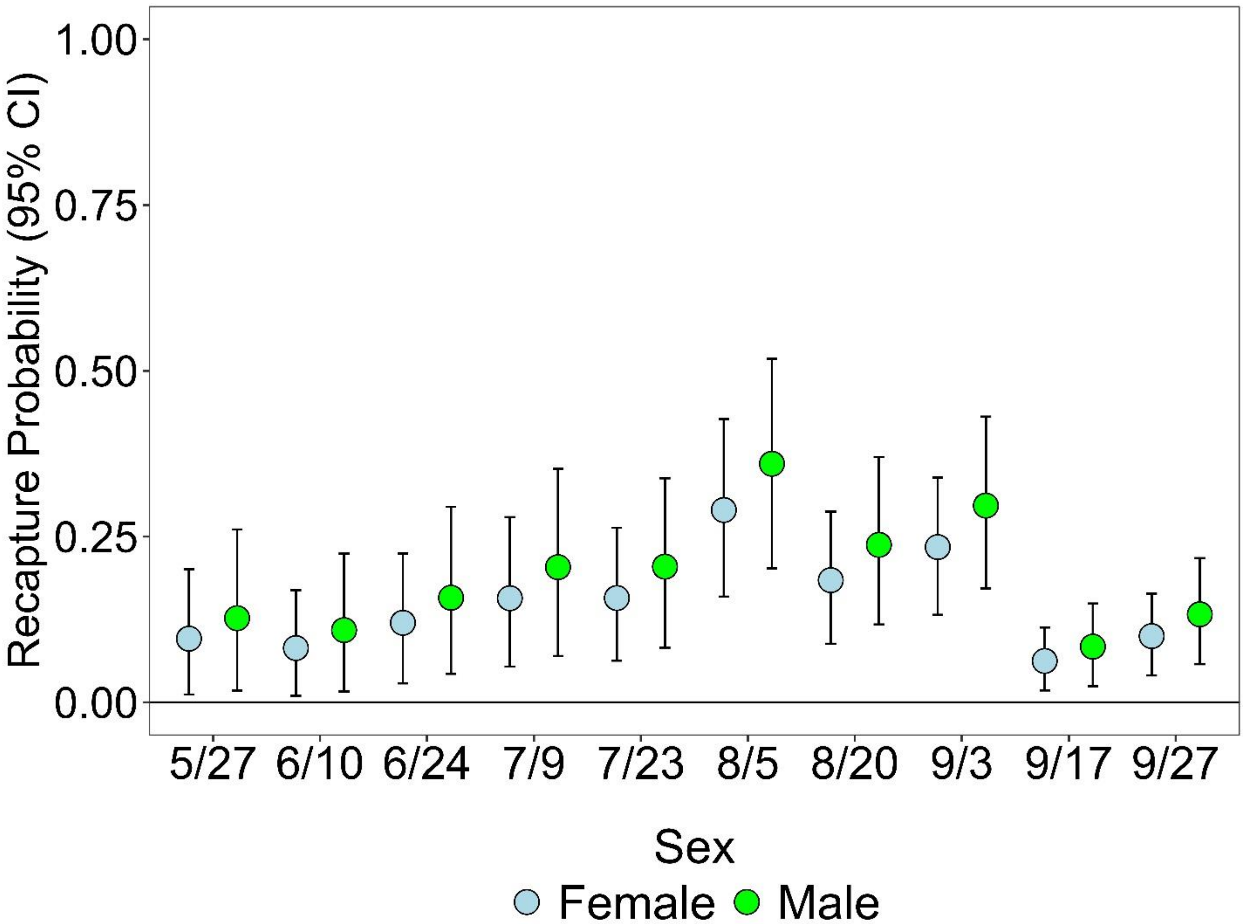
Annual apparent survival was higher for females (0.72, 95% HPDI = 0.63–0.81) than for males (0.58, 95% HPDI = 0.44–0.72) although the 95% HPDI overlapped broadly. Mean annual recapture probability was higher for males (0.35, 95% HPDI = 0.07–0.70) than for females (0.18, 95% HPDI = 0.03–0.36) although the 95% HPDI overlapped broadly. Posterior means for annual recapture probabilities ranged from 0.08–0.61 for males and 0.04–0.40 for females (Figure 5).

Figure 5. Year-specific annual recapture probabilities and 95% highest posterior density intervals for northern Mexican gartersnakes in the upper Santa Cruz River of the San Rafael Valley, Arizona, during 2012-2023 (recapture probability not estimated for 2008 because it was the first year of mark-recapture surveys).



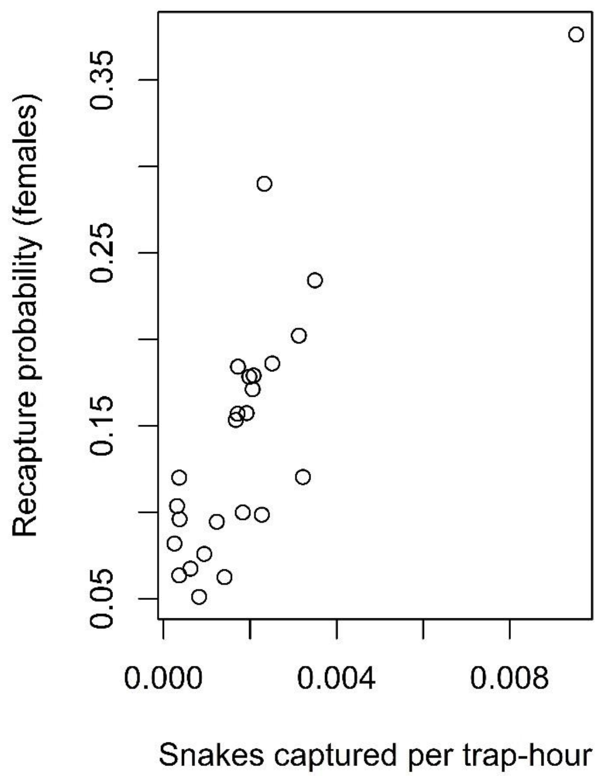
Mean recapture probability across sessions was also higher for males (0.16, 95% HPDI = 0.09–0.24) than for females (0.12, 95% HPDI = 0.07–0.17) although the 95% HPDI overlapped broadly. Session-specific recapture probabilities across the entire study ranged from 0.07–0.45 for males and 0.05–0.38 for females. There was also little consistent seasonal variation in trip-specific recapture probability during 2023 (Figure 6).

Figure 6. Session-specific recapture probabilities and 95% highest posterior density intervals for northern Mexican gartersnakes in the upper Santa Cruz River of the San Rafael Valley, Arizona, during 2023.



Session-specific recapture probability was positively correlated with snakes captured per trap-hour ($r = 0.77$, $P < 0.0001$; Figure 7).

Figure 7. Relationship between catch-per-unit-effort (snakes captured per trap-hour) and trip-specific recapture probabilities for northern Mexican gartersnakes in the upper Santa Cruz River of the San Rafael Valley, Arizona, during 2023.



Radio Telemetry. We attached radio transmitters to 16 individual NMGS throughout the study. We attached GPS transmitters to 13 individuals, implanted VHF transmitters into two individuals, and attached both transmitters (on separate occasions) to one individual. We attached GPS transmitters only to females, because of their larger body size, and VHF transmitters only to males. The individual that received both transmitter types was a female. We re-attached new GPS transmitters to five individuals between one and four times. We were successfully able to recapture snakes with GPS transmitters on eight occasions before the transmitter's battery died. Additionally, we had snakes shed GPS transmitters off on nine occasions and GPS transmitters became unattached for unknown reasons on four occasions. We had GPS transmitters malfunction on two occasions but were able to relocate the snake and transmitter on one of those occasions. On one occasion, the GPS transmitter battery died before we could recover it or the snake.

We obtained a total of 4,917 GPS fixes with a mean of 289.24 ± 18.74 fixes (range: 151-408 fixes) per tracking period. Only 34.33% were of sufficient quality based on the HDOP value and the number of satellites obtained while 50.4% of the fixes did not obtain any satellites. It took transmitters a mean of 7.55 ± 0.19 seconds to take a fix. NMGS moved a mean distance of 7.85 ± 0.38 meters between consecutive hourly fixes. The maximum documented hourly movement by GPS-telemetered NMGS was 135.71 m (Table 3). Mean space use estimates during all of a GPS-telemetered individual's tracking periods was 0.60 ± 0.19 hectares (range: 0.14-1.52 ha; Figures 8–17). Space use estimates from VHF-telemetered individuals were 0.57 ha by a female, 0.90 ha by a male, and 0.15 ha by a male NMGS (Table 4; Figure 18).

Table 3. GPS transmitter deployment and movement summary statistics from female northern Mexican gartersnakes in the upper Santa Cruz River of the San Rafael Valley, Arizona, USA, during 2023. GPS locations were recorded hourly and good locations were defined as those with a horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites. Space use was estimated using minimum convex polygons. Time to take a fix refers to the time it took the unit to obtain sufficient satellites to record a location.

Telemetry ID	Attachment #	Days deployed	Number of good locations (HDOP ≤ 5, Satellite ≥ 5)	100% MCP size (ha)	Mean distance between fixes (m)	Max distance between fixes (m)	Mean time to take a fix (sec)
T001	1	11	167	0.24	6.42	23.89	6.94
T001	2	12	110	0.84	8.06	37.88	8.04
T001	3	9	110	0.09	6.27	19.97	7.59
T001	4	14	73	0.63	10.57	29.60	7.39
T001	5	9	42	0.07	8.11	41.01	6.78
T002	1	14	113	0.60	6.94	24.22	7.21
T002	2	18	127	0.74	8.32	50.76	6.76
T003	2	14	112	1.16	10.92	135.71	8.37
T003	3	18	140	0.27	9.48	50.40	7.79
T005	1	7	53	0.20	8.37	15.85	8.76
T006	2	13	165	0.24	7.74	35.82	9.11
T006	3	8	129	0.04	5.54	15.91	8.47
T010	1	15	117	0.23	6.61	16.35	7.49
T011	1	12	37	0.15	6.25	15.24	6.82
T012	1	17	82	0.41	8.80	44.05	7.65
T015	1	15	103	0.14	7.27	60.38	6.52

Table 4. Sex, total number of days tracked, total number of good GPS locations (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites), and total minimum convex polygon (MCP) size for northern Mexican gartersnakes monitored with GPS and VHF transmitters along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during 2023. Individuals with VHF transmitters are denoted with an "i" at the start of their Telemetry ID.

Telemetry ID	Sex	Total Days Monitored	Total Number of Good Fixes	Total 100% MCP Size (ha)
T001	Female	55	502	1.41
T002	Female	32	240	1.07
T003	Female	32	252	1.52
T005	Female	7	53	0.20
T006	Female	21	294	0.30
T010	Female	15	117	0.23
T011	Female	12	37	0.15
T012	Female	17	82	0.41
T015	Female	15	103	0.14
iT004	Female	62	41	0.57
iT008	Male	62	40	0.90
iT009	Male	31	21	0.15

Figure 8. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T001) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during five attachment periods in 2023 (1st: orange; 2nd: purple; 3rd: blue; 4th: green; 5th: red). The 100% minimum convex polygon (MCP, red line) across all good GPS fixes is shown by the red outline. The size of each fix's location indicates the number of fixes received at that location.

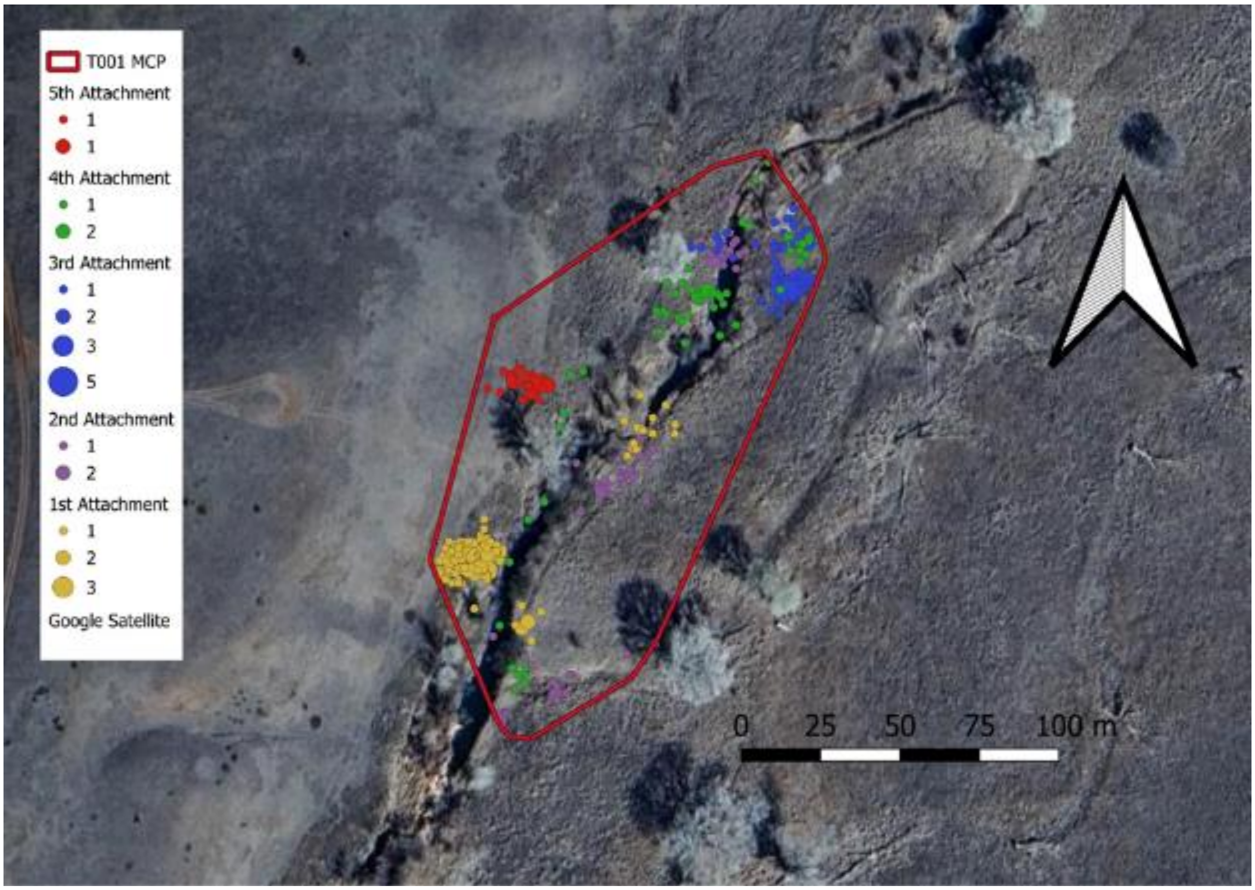


Figure 9. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T002) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during her two attachment periods in 2023 (1st: red; 2nd: green). The 100% minimum convex polygon (MCP, red line) across all good GPS fixes is shown by the white outline. The size of each fix's location indicates the number of fixes received at that location.

Figure 10. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T003) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during her two attachment periods in 2023 (1st: red; 2nd: green). The 100% minimum convex polygon (MCP, red line) across all good GPS fixes is shown by the white outline. The size of each fix's location indicates the number of fixes received at that location.

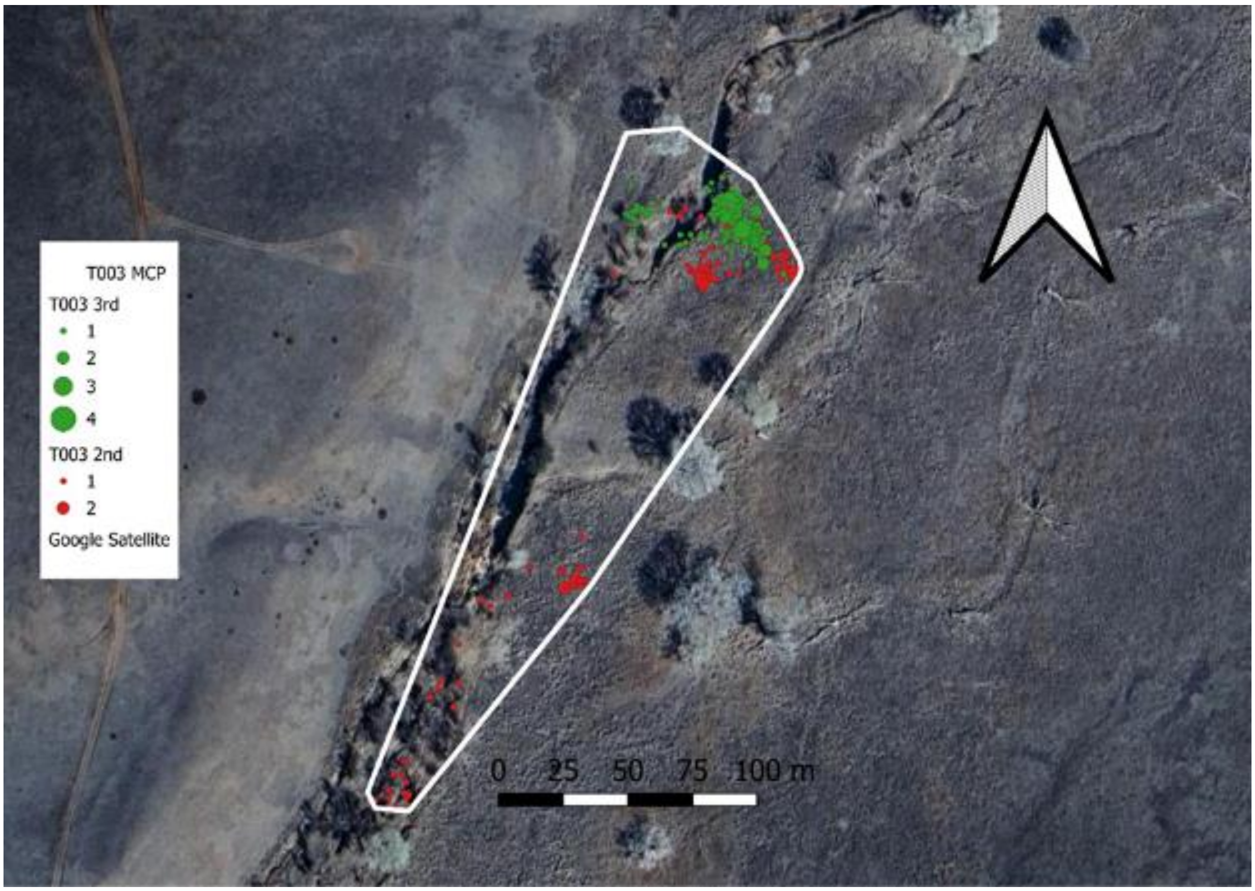


Figure 11. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T005) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during her one attachment period in 2023 (red points). The 100% minimum convex polygon (MCP, red line) across all good GPS fixes is shown by the red outline. The size of each fix's location indicates the number of fixes received at that location.

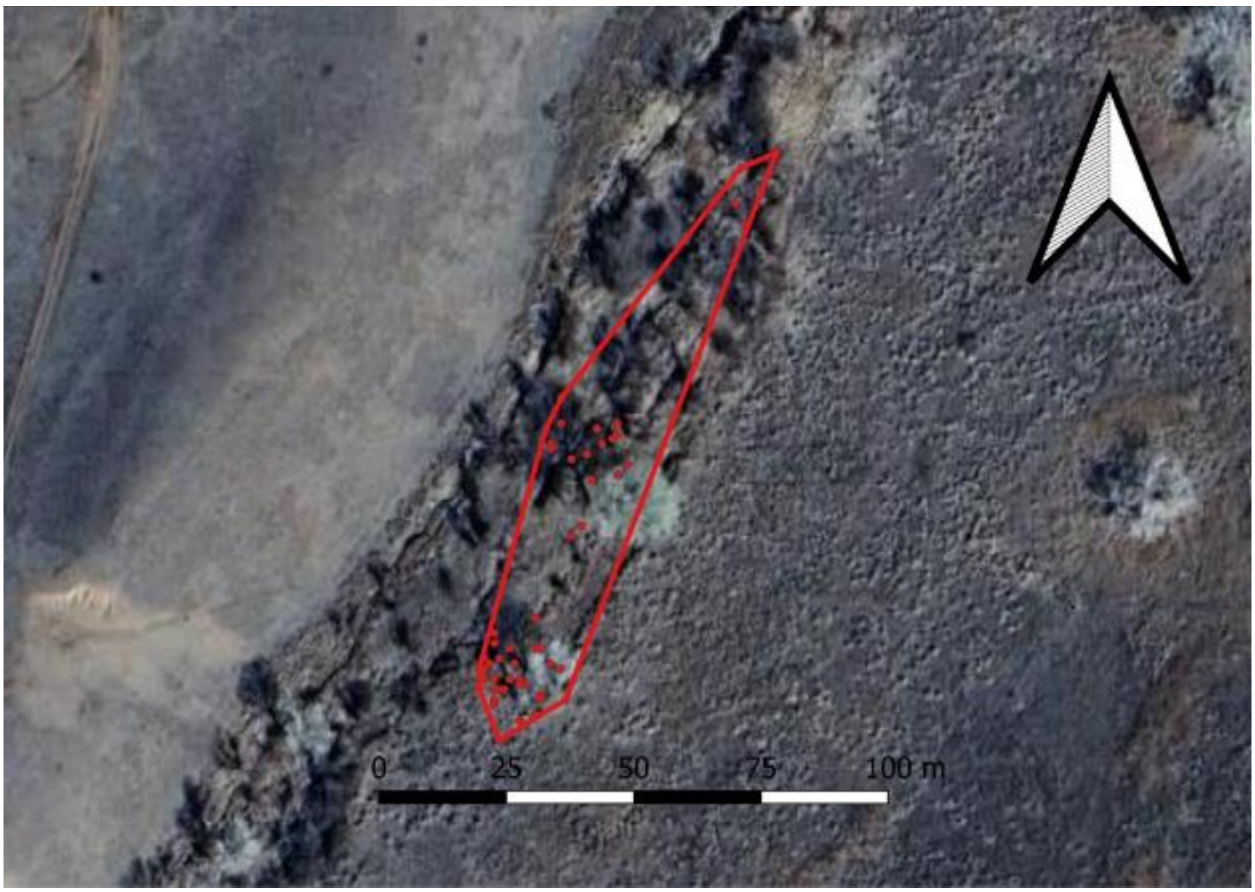


Figure 12. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T006) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during her two attachment periods in 2023 (1st: red; 2nd: green). The 100% minimum convex polygon (MCP, red line) across all good GPS fixes is shown by the white outline. The size of each fix's location indicates the number of fixes received at that location.

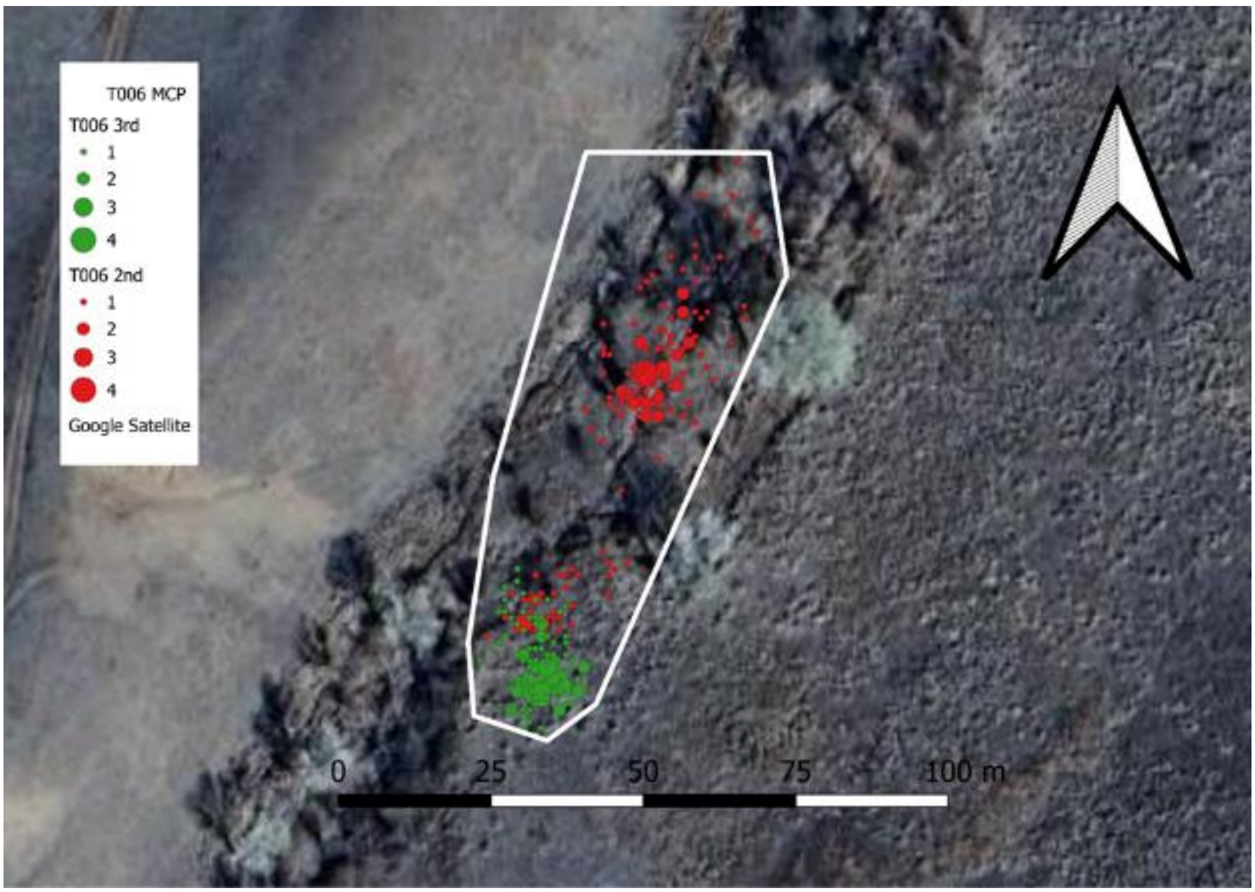


Figure 13. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T010) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during her one attachment period in 2023 (red points). The 100% minimum convex polygon (MCP, red line) across all good GPS fixes is shown by the red outline. The size of each fix's location indicates the number of fixes received at that location.

Figure 14. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T011) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during her one attachment period in 2023 (red points). The 100% minimum convex polygon (MCP, red line) across all good GPS fixes is shown by the red outline. The size of each fix's location indicates the number of fixes received at that location.

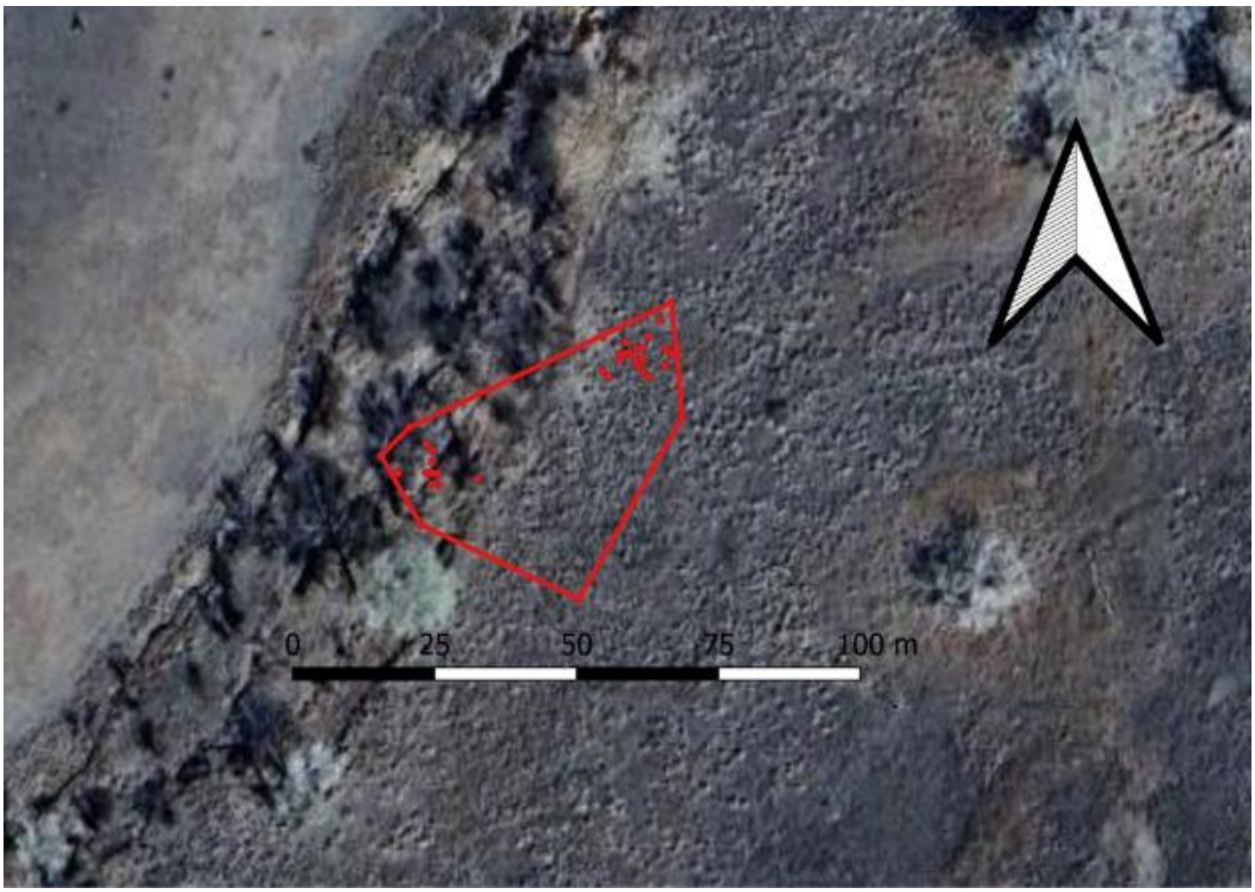


Figure 15. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T012) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during her one attachment period in 2023 (red points). The 100% minimum convex polygon (MCP, red line) across all good GPS fixes is shown by the red outline. The size of each fix's location indicates the number of fixes received at that location.

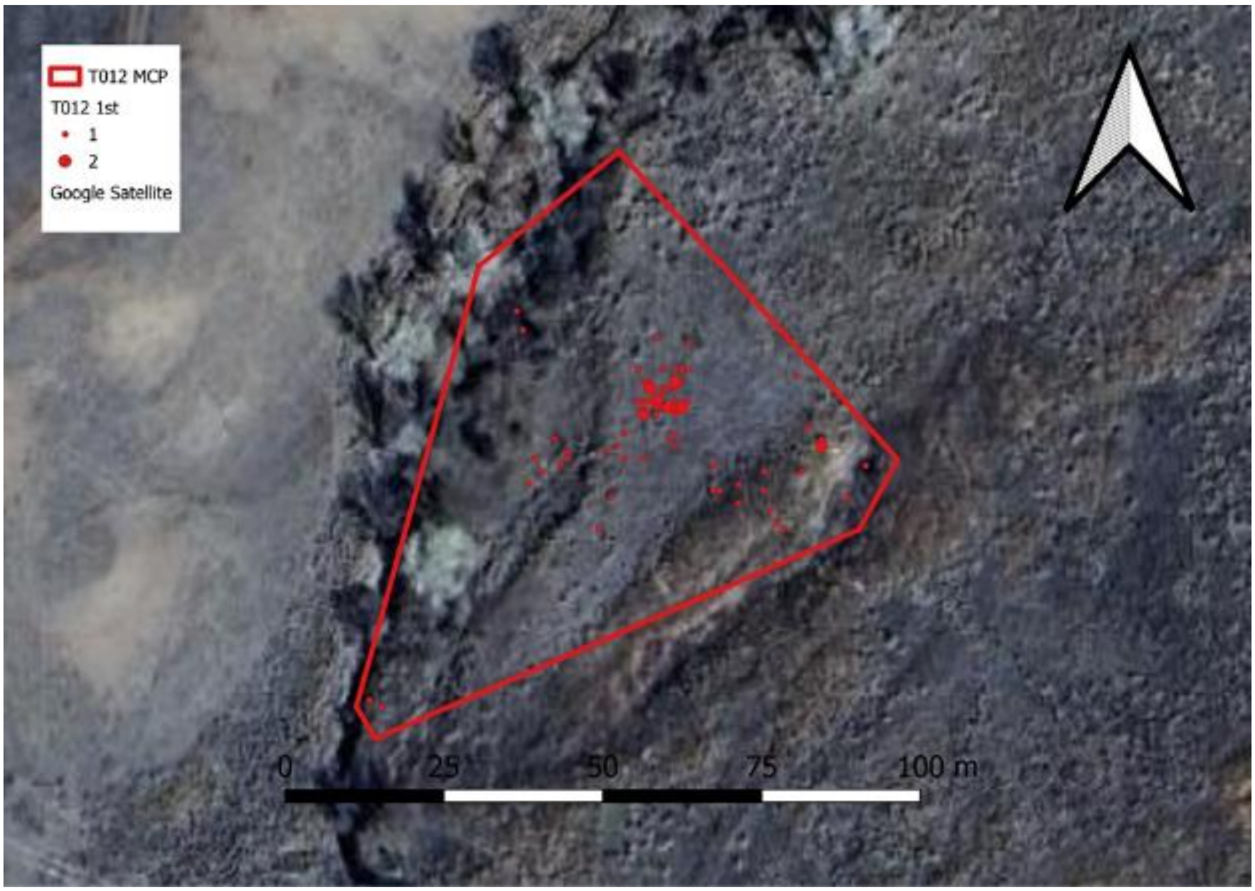


Figure 16. Map of good GPS fixes (horizontal dilution of precision (HDOP) ≤ 5 and those that connected to ≥ 5 satellites) for a female northern Mexican gartersnake (T015) along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during her one attachment period in 2023 (red points). The 100% minimum convex polygon (MCP, white line) across all good GPS fixes is shown by the white outline. The size of each fix's location indicates the number of fixes received at that location.

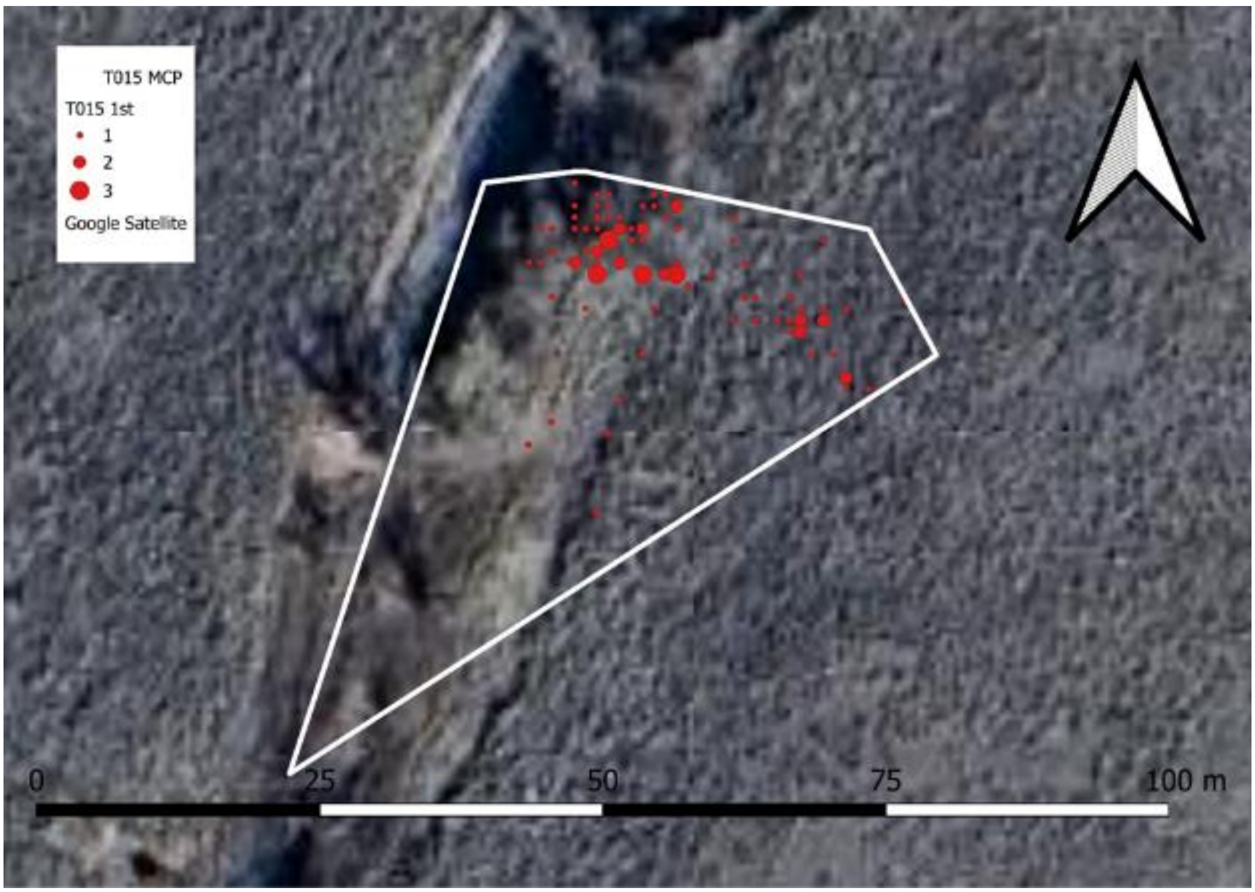


Figure 17. Map of cumulative 100% minimum convex polygons for northern Mexican gartersnakes tracked during 2023 using GPS transmitters along the upper Santa Cruz in the San Rafael Valley, Arizona, USA.

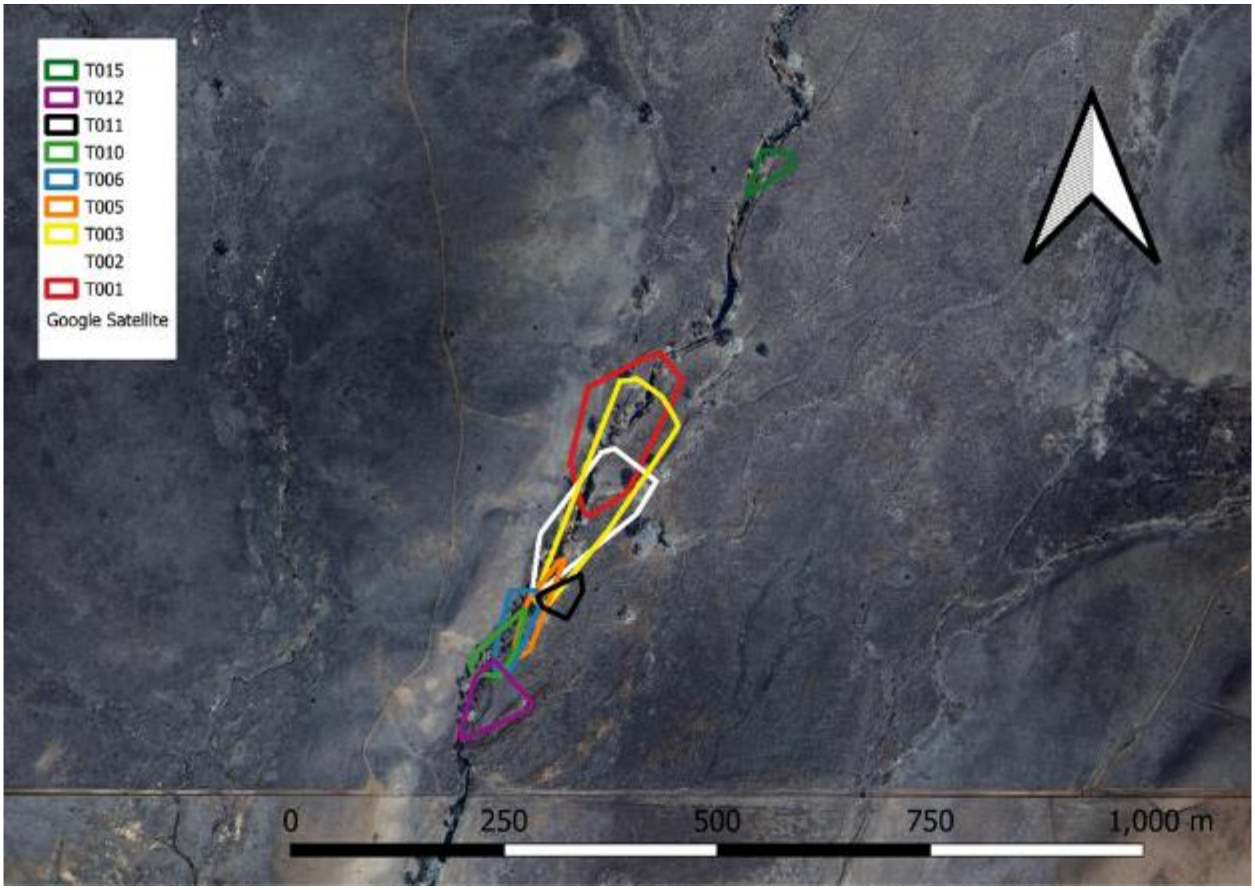
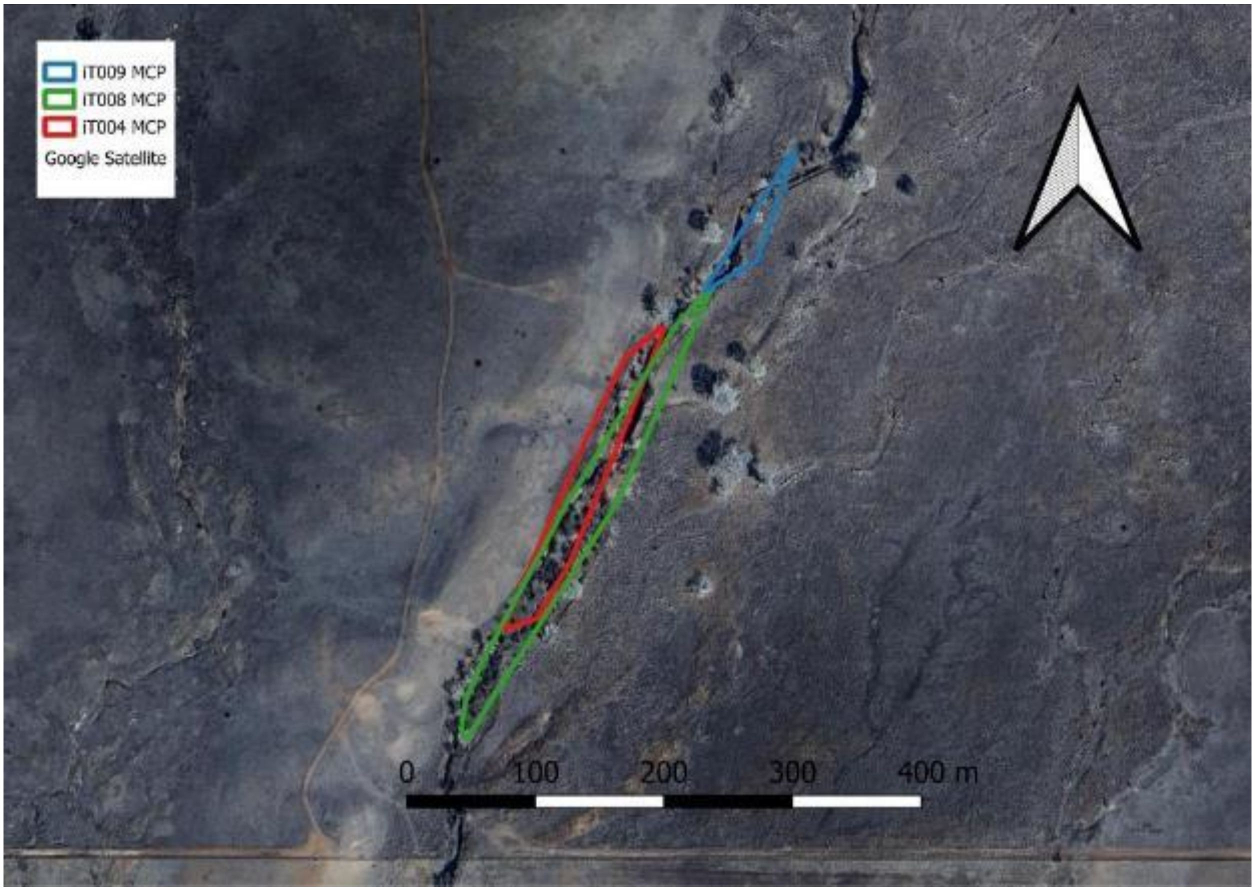


Figure 18. Map of cumulative100% minimum convex polygons (MCP) for northern Mexican gartersnakes tracked using VHF transmitters along the upper Santa Cruz River in the San Rafael Valley, Arizona, USA, during 2023.



Discussion

Our results add to the growing body of knowledge of NMGS in grassland landscapes of southeastern Arizona and provide the first model-based survival estimates for this species. Our survival estimates, 0.72 for females and 0.58 for males, are largely consistent with those reported for other *Thamnophis* species, including the federally endangered San Francisco gartersnake (*T. sirtalis tetrataenia*) and giant gartersnake (*T. gigas*) (Table 5). This is noteworthy because the upper Santa Cruz River contains abundant non-native fish (e.g., largemouth bass) and bullfrogs, which may compete for food resources or predate small NMGS. Predation by non-native bullfrogs on small-bodied *Thamnophis* has been noted in western North America including *T. gigas* in California (Wylie et al. 2003), *T. ordinoides*, *T. sirtalis*, and *T. elegans* in British Columbia (Jancowski and Orchard 2013), *T. cyrtopsis* in Arizona (E. Sudbeck, personal communication), and NMGS in Arizona (Boyarski et al. 2015), and there are instances of largemouth bass predating NMGS (Young and Boyarski 2013). It is unclear how frequent *Thamnophis*, and more specifically NMGS, are preyed on by bullfrogs or non-native fish, but it appears to be a relatively rare occurrence. For example, Jancowski and Orchard (2013) analyzed stomach contents from 5,075 bullfrogs in British Columbia and recorded 11 cases of predation on three *Thamnophis* species, and out of 89 bullfrog stomachs examined at a site in central Arizona 2 NMGS were found (Ryan, unpubl.). In contrast, NMGS regularly prey upon bullfrogs where the species cooccur (Emmons and Nowak 2016b, Boyarski et al. 2019, Nowak et al. 2019) and we documented multiple instances of NMGS in our study eating larval and metamorphosed bullfrogs. Furthermore, we captured both adult and juvenile NMGS during most trapping sessions and, during 2023, we captured neonate NMGS regularly from 11 July through 26 September. Our estimated survival rates and the long-term presence of juveniles and neonates indicates the presence of a robust NMGS population in the upper Santa Cruz River in the San Rafael Valley. These finding are consistent with the NMGS population at Bubbling Ponds in central Arizona, that also appears robust while in the presence of large numbers of bullfrogs and non-native fish (Boyarski et al. 2015, Boyarski et al. 2019).

Table 5. Annual apparent survival (Φ) estimates from other Thamnophis species estimated using mark-recapture data and survival models. Survival estimates are reported with 95% confidence/credible intervals (CI) or ± 1 standard error. SVL is snout-vent length.

Common Name	Scientific Name	Survival Estimate	Location	Study	Notes
San Francisco Gartersnake	*T. sirtalis tetrataenia*	2008–2009: 0.88 (0.67-1.00) 2009–2010: 0.82 (0.55-0.99)	San Mateo Co., CA	Halstead et al. (2011)	Two different time periods
Giant Gartersnake	*T. gigas*	181 mm SVL: 0.37 (0.19-0.59) 1144 mm SVL: 0.73 (0.54-0.87)	Central Valley, CA	Hansen et al. (2015)	Smallest and largest individuals
Giant Gartersnake	*T. gigas*	Colusa NWR West: 0.59 (0.47–0.73) Natomas 1: 0.35 (0.17–0.56)	Central Valley, CA	Rose et al. (2018)	Highest and lowest site-specific *Φ* estimates
Western Terrestrial Gartersnake	*T. elegans*	L1: 0.34–0.40 L2: 0.55–0.57 M3: 0.71–0.76 M1: 0.74–0.78 M2: 0.76–0.86	Lassen Co., CA	Bronikowski and Arnold (1999)	Upper and lower 95% CI by population (L, lake; M, mountain)
Oregon Gartersnake	*T. atratus hydrophilus*	Males: 0.56 ± 0.03 Females: 0.64 ± 0.02	Del Norte Co., CA	Lind et al. (2005)	
Plains Gartersnake	*T. radix*	Males Age 0: 0.17 (0.07–0.33) Females Age 0: 0.16 (0.07–0.33) Males Age 1: 0.42 (0.29–0.56) Females Age 0: 0.41 (0.28–0.55) Males Age 4+: 0.37 (0.16–0.64) Females Age 4+: 0.45 (0.21–0.71)	DeKalb Co., IL	Stanford and King (2004)	Model-averaged *Φ* estimates and 95% CI

Catch-per-unit-effort continued to vary markedly within and among years although we found evidence that trap success was greatest during July through September. This coincides with the summer monsoon, when rainfall reaches its peak, and temperatures are favorable for the above-ground activity of snakes. Boyarski et al. (2019) noted higher relative detection probabilities of NMGS at the Bubbling Ponds Fish Hatchery during June-September compared to May. Our 2023 results also indicate that trapping success varied by habitat type with greater trapping success in habitat types with relatively low water levels compared to pools. We also captured more NMGS immediately following drying around traps. The 2023 monsoon season featured below-average rainfall levels and we accordingly noticed a progressive drying of our survey reach as the summer progressed. Lowering water levels may have concentrated NMGS to a greater degree and increased their likelihood of encountering and entering a trap. Finally, Lind et al. (2005) also reported a strong positive correlation between CPUE and model-based recapture probabilities (r = 0.728).

We generally captured more female than male NMGS. Boyarski et al. (2019) noted a similar bias towards female captures for NMGS although Halstead et al. (2011) reported a sex ratio for San Francisco gartersnakes that did not differ significantly from 1:1. Shonfield et al. (2019) reported a slightly male-biased sex ratio (158:188 F:M; $\chi^2 = 2.60$, $P = 0.1068$) for Butler's gartersnakes (*Thamnophis butleri*) in Ontario, Canada. Welsh et al. (2010) reported an approximately equal sex ratio in adult Oregon gartersnakes (*Thamnophis atratus hydrophilis*) in northwestern California (96:110 F:M; $\chi^2 = 0.95$, $P = 0.3293$). The higher female:male capture ratio may reflect: 1) behavioral differences between sexes that lead to females being more likely than males to enter traps, 2) higher female survival (although there was substantial uncertainty in our apparent survival estimates), or 3) higher male emigration (the Cormack-Jolly-Seber model cannot distinguish between mortality and permanent emigration). Additional research is needed to evaluate which of these three hypotheses are responsible for the high female:male capture ratio. Welsh et al. (2010) found that dispersal rates were male-biased in the Oregon gartersnake. The similar recapture probabilities for males and females indicated that marked males are just as likely to be recaptured as marked females.

Our GPS telemetry data did not document any long-distance movements by NMGS and indicated that all telemetered individuals remained within approximately 100 m of the river. However, we documented individuals moving up to approximately 400 m along the river itself.

Our observations are consistent with observations from Emmons (2017) who reported that 89% of VHF telemetry observations of NMGS along the Verde River during the active season were in terrestrial habitat and averaged 14.7 m (range = 0-152 m) from water. Boyarski et al. (2015) also found that VHF-telemetered NMGS at Bubbling Ponds used pond edges and fallow ponds significantly more than expected based on availability although upland habitats were used significantly less than expected based on availability. However, during 2022, we documented an apparent 705 m movement made by an adult female NMGS between 1700-1800 h on 9 September from the river to adjacent upland grassland, although we did not get a GPS location at 1900 h to indicate how long this individual remained in the upland (M. Goode, unpublished data). However, the next GPS location with HDOP ≤5 was the following morning at 0900 (10 September) and showed that the snake had returned to near the river. The HDOP values for the 1700 h and 1800 h fixes were 1.4 and 1.8, respectively, indicating high-quality coordinates for these locations. The 1700 h location was based on signals from five of five satellites; however, the 1800 h location was based on only 3 of 3 satellites. In any case, results from our test PinPoint transmitter suggest that this long-distance movement was unlikely the result of a signal error. Hence, NMGS from the upper Santa Cruz River may make longer movements into upland habitats, particularly during the monsoon when temporary standing water may be more extensive in the San Rafael Valley. Greater prevalence of standing water may facilitate NMGS movement by lowering the risk of desiccation and/or greater availability of potential prey (e.g., amphibians) although additional research is needed to test these hypotheses.

Previous tests evaluating the accuracy and precision of PinPoint beacon GPS locations during 2022 demonstrated that these transmitters are unable to record GPS coordinates underwater or in thick vegetation (M. Goode, unpublished data), which may limit their utility for collecting relatively fine-scale movement data. A PinPoint beacon placed in an open grassy slope had 71.9% and 95.2% of coordinates with HDOP ≤5 within 5 and 10 m of the centroid of the coordinates (M. Goode, unpublished data). Additional field testing with PinPoint beacons, placed in a wide variety of microhabitats, could help better understand the conditions under which one is unlikely to obtain coordinates or when coordinate quality becomes unsuitable for analyses. Combining transmitter temperature readings recorded by PinPoint transmitters with GPS beacon data may also yield greater insights into NMGS movement ecology. For example, the first high-quality GPS coordinate collected during the day regularly corresponded to a sharp increase in transmitter temperature, a pattern consistent with snake basking behavior.

While the ability to collect and store GPS coordinate data is a valuable asset of the PinPoint transmitters, this must be weighed against battery life limitations. Users have tremendous flexibility in programming both the GPS and VHF schedules using Lotek's PinPoint Host software to optimize battery life. The schedules that we used (hourly GPS fixes; VHF transmission and RF communication every five hours, and activity data every two hours) were predicted by this software to allow the transmitters to last 20 days on average (13 days under worst-case scenario operating life). Increasing the GPS location frequency to 2, 3, 4, 5, 6, and 12 hours resulted in worst-case operating life scenarios of 20, 25, 28, 29, 31, and 36 days, respectively. PinPoint Host did not allow us to calculate a battery life estimate with a single GPS location per 24 hours. Reducing the absolute number of GPS locations collected during a 24-hour period would provide additional gains in battery life. For example, collecting hourly GPS locations only between 1000 and 1800 predicted a worst-case scenario of 21 days (vs. 13 days under hourly locations over an entire 24-hour period). In contrast, NMGS are large enough to carry implanted VHF transmitters with expected one-year battery lives (Emmons 2017, Myrand 2019).

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trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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