Population ecology of the federally threatened narrow-headed gartersnake (*Thamnophis rufipunctatus*) in Canyon Creek, Arizona

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Final Report for Research Work Order AZ-81

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Narrow-headed Gartersnake (photo by Javan Bauder)

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Abstract

The narrow-headed gartersnake (*Thamnophis rufipunctatus)* is a federally threatened species endemic to the Mogollon Rim in central Arizona and western New Mexico. This species has declined across its range primarily due to habitat loss, degradation and invasive species. Additional information on this species' ecology, particularly empirical estimates of movement and demographic parameters, are particularly important for its management and conservation. We conducted a three-year mark-recapture study of narrow-headed gartersnakes in Canyon Creek in central Arizona to address the following objectives: (1) conduct three active seasons of intensive field sampling for narrow-headed gartersnakes; (2) use newly collected mark-recapture data to estimate survival and abundance; and (3) successfully implant harmonic transponder tags into syntopic western terrestrial gartersnakes (*Thamnophis elegans*), a non-threatened species, and, conditional upon this success, implant these tags into juvenile and adult narrow-headed gartersnakes in Canyon Creek to monitor space use and habitat selection. We used radio transmitters attached externally to document gartersnake movements due to their technological advantages to harmonic transponder tags. However, transmitters did not remain attached to gartersnakes long enough to collect meaningful movement data. We were, however, able to obtain meaningful movement data using recaptures of marked gartersnakes. We also compared capture rates, individual growth rates, movement, and apparent survival estimates between narrow-headed gartersnakes and western terrestrial gartersnake to provide a better understanding of their comparative ecology. We also documented the successful application of passive PIT tag arrays for monitoring PIT-tagged gartersnakes. While we captured more western terrestrial gartersnakes during our study, we did not find marked differences between these two species in individual growth rates, movement patterns, recapture probabilities, and apparent survival. We provide abundance estimates and their 95% credible intervals for both narrow-headed and western terrestrial gartersnakes, although data sparsity and tenuous model assumptions call for extreme caution when interpreting our abundance estimates. Our results fill geographical and ecological gaps in our knowledge of narrow-headed gartersnakes and can provide a foundation for future long-term monitoring studies at Canyon Creek.

Introduction

Many species are threatened by anthropogenic disturbances, including habitat loss, fragmentation, invasive species, and climate change, and these threats may lead to population declines (Gaind 2016). However, species vary widely in their responses to disturbances due to variation in behavioral and ecological traits including variation in geographic range (Gaston and Blackburn 1995), space-use requirements (Woodroffe and Ginsberg 1998), habitat specificity (Reinhardt et al. 2005), social structure (Courchamp et al. 1999), foraging mode (Salt 1967, Andrews 1979), and growth (Schoener 1971, Gerritsen and Strickler 1977, Huey and Pianka 1981, Webb et al. 2003). Life history variation can also strongly influence susceptibility to anthropogenic disturbances. For example, many species have ‘slow’ life-histories (e.g., slow growth rate, late age at maturation, high adult survival, and low lifetime reproductive output), which may put them at increased risk of anthropogenically induced population declines (Webb et al. 2002, Holliday 2005, Waldron et al. 2013, Brown 2016). Identifying the links between species life history, ecology, and susceptibility to population declines and extirpation is important for both identifying at-risk species but also for understanding the factors contributing to their at-risk status (Caughley 1994, Webb et al. 2002, Robinson 2006, Hernández-Yáñez et al. 2022). Further, this information is important for developing species conservation and management plans (Robinson 2006, Waldron et al. 2006), which is critical for declining and sensitive species (Mawdsley et al. 2009).

Comparative ecological studies among closely related and sympatric species can help elucidate species-specific risk factors especially in cases where species differ in their degree of imperilment. Snakes are a good taxon for such comparisons because local snake communities often support multiple congeneric species that differ in prey preferences, foraging behavior, habitat associations, and demographic traits (Parker and Plummer 1987, Steen et al. 2007, 2014, Durso et al. 2013). Previous studies have reported interspecific differences in imperilment status between closely related sympatric snake species which have been linked to differences in life history and ecology (Roe et al. 2004, Waldron et al. 2006). However, such comparisons are often hampered by a lack of basic natural history information for many snake species due to their cryptic nature (Steen 2010, Durso et al. 2011). Furthermore, ecological traits and demographic parameters within a single snake species can vary among populations due to local differences in thermal environments, habitat conditions, and disturbance levels (Bronikowski 2000, Jenkins et al. 2009, Gomez et al. 2015).

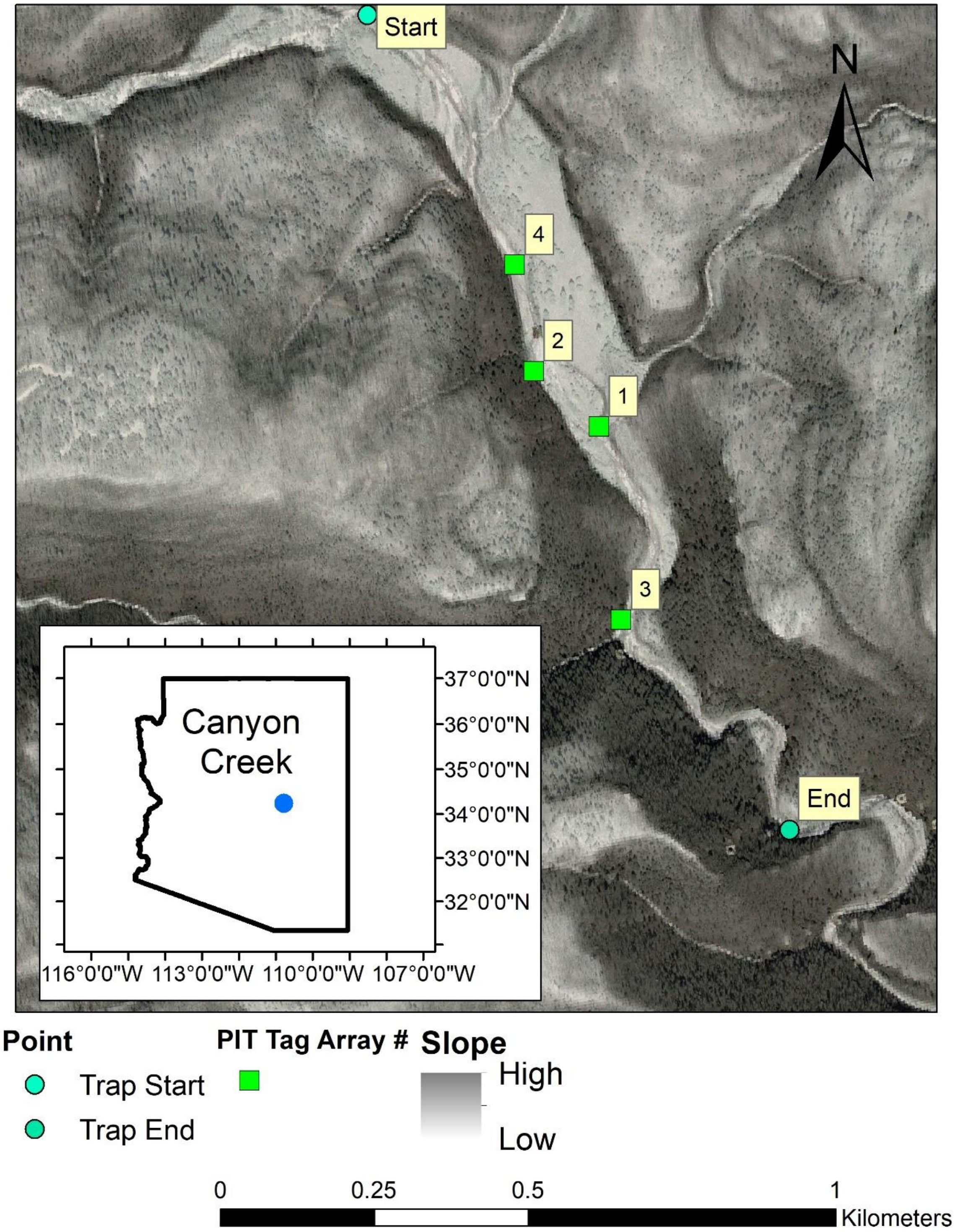
Gartersnakes (*Thamnophis* spp.) are a widespread genus of natricine snake across western North America (Stebbins 2003) and a single site often supports multiple species (Hebard 1951, White and Kolb 1974, Engelstoft and Ovaska 2000, Manier and Arnold 2005). For example, five gartersnake species are found within Arizona in the southwest USA and these species differ in the extent of their geographic distribution, biology, and imperilment status (Holycross et al. 2022). Three of these species have been recorded as occurring in sympatry in Arizona. One is the narrow-headed gartersnake (*Thamnophis rufipunctatus*, hereafter THRU), which is endemic to the Mogollon Rim of central Arizona and western New Mexico (Holycross et al. 2020). THRU is semiaquatic and occurs primarily along and near perennial, mid- to high elevation streams typically from 1200–1900 m but have been recorded as low as 750 m and as high as 2430 m (Holycross et al. 2020). THRU preys primarily upon native fish using ambush foraging while submerged lying on the stream bottom or using a semi-prehensile tail to anchor themselves to the stream bottom or edge and is more aquatic in their foraging and diet than other *Thamnophis* species (Fleharty 1967, Holycross et al. 2020). However, little additional published information exists on THRU life history and ecology, particularly empirical estimates of demographic parameters (e.g., survival). These knowledge gaps are particularly important because THRU is federally threatened having experienced population declines and/or extirpation from many historical locations, which have been attributed to loss or degradation of riparian and within-stream habitat and invasive aquatic species (e.g., fish, crayfish) (USFWS 2014, Holycross et al. 2020). In contrast, the western terrestrial gartersnake (*T. elegans*, hereafter THEL), while largely sympatric with THRU within Arizona and New Mexico, has a much wider distribution that spans much of western North America and is not of conservation concern (Stebbins 2003, Hallas et al. 2021). In Arizona, THEL inhabits a broad range of elevations and plant communities, from Great Basin Desertscrub to Rocky Mountain Montane Conifer forest; although the species is associated with riparian and wetland environments, they use a much broader diversity of environments including ponds, stock tanks and streams and intermittent water sources (Drost 2020). THEL are generally associated more with terrestrial environments than other *Thamnophis* species (Drost 2020). THEL also consume a wider diversity of prey, including invertebrates, fish, anurans, lizards, and small mammals (Kephart 1982, Kephart and Arnold 1982, Drost 2020). The black-necked gartersnake (*T. cyrtopsis*, hereafter THCY) also occurs throughout central and southern Arizona and is not of conservation concern (Holycross et al. 2022). THCY typically occupies lower elevation areas, but has been documented up to 2050 m in Arizona (Jones and Hensley 2020). THCY is most commonly associated with riparian and aquatic environments and has a diverse diet including anurans, fish and invertebrates (Jones and Hensley 2020, Holycross et al. 2022).

We compared the ecology of syntopic gartersnakes at one site in central Arizona that supports THRU, THEL, and THCY. Our goal was to provide biological and demographic information for these species and compare these traits. Our specific objectives were to: (1) conduct three active seasons of intensive field sampling for THRU at Canyon Creek, Arizona; (2) use newly collected mark-recapture data to estimate survival and abundance; and (3) successfully implant harmonic transponder tags into THEL and, conditional upon success, implant these tags into juvenile and adult THRU in Canyon Creek to monitor space use and habitat selection. Harmonic transponder (HT) tags are very small (0.03 g) tags that emit a signal in response to a hand-held transponder unit. We initially considered using HT tags because they have been successfully used as external attachments for tracking small herpetofauna (M. Ryan, Arizona Game and Fish Department, personal communication), but these tags have notable drawbacks in their use compared to traditional very high frequency (VHF) radio transmitters. Specifically, HT tags have a signal range of 10-30 m and do not have uniquely identifiable frequencies which makes it difficult to determine the identity of the individual being tracked. Following the initiation of this study in 2022 we received permission from the U.S. Fish and Wildlife Service to attach VHF transmitters externally to THRU and THEL to monitor their movements.

Study Site

We studied along a ca. 1.7 km reach (hereafter survey reach) of Canyon Creek (ca. 1900 m elevation), a spring-fed tributary of the Salt River, in Gila County, Arizona, flowing south from the Mogollon Rim (Figure 1). Our survey reach was located on the Pleasant Valley Ranger District in the Tonto National Forest and bounded on the downstream end by the White Mountain Apache Reservation. Our survey reach had been surveyed previously for THRU yet previous surveys did not uniquely mark captured gartersnakes (Ryan et al. 2019). Vegetation communities in and around our study area included transition zones between Rocky Mountain (Petran) Montane Conifer Forests and Great Basin Conifer Forests (Brown and Lowe 1995) and riparian communities. Upland communities were dominated by Ponderosa pine (*Pinus ponderosa*) with a mix of juniper (*Juniperus*), white (*Abies concolor*), and Douglas fir (*Pseudotsuga menziesii*). Riparian tree species included willows (*Salix* spp.) and narrowleaf cottonwood (*Populus angustifolia*).

Figure 1. Map of the study site location within Arizona and zoomed in section of the study site at Canyon Creek, Arizona. The locations of start and end of survey reach, and the passive PIT antennas are noted.



The Canyon Creek fish community consists of four species, two native species, Speckled Dace (*Rhinichthys osculus*) and Desert Sucker (*Catostomus clarkii*) and two nonnative, sportfish species, Brown Trout (*Salmo trutta*) and Rainbow Trout (*Oncorhynchus mykiss*), although the latter species is very rare in the study stretch (Cole 2023). No nonnative crayfish are present at Canyon Creek, although the nonnative and invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) was detected in April 2023 and quickly became abundant in the survey stretch.

Methods

Field surveys

We surveyed for gartersnakes using a combination of visual encounter surveys (VES) and trapping. We surveyed 3–4 multiday survey/trapping sessions (hereafter survey sessions; 2–8 nights per session, mean ~5 nights per session) during May–August 2022–2024. We conducted VES with multiple (2–7) surveyors by systematically walking the streamside and turning all moveable cover objects (e.g., rocks, logs). All cover objects were returned to their original position. We recorded start and end coordinates and time and the number of people participating in each VES. We alternately began VES at each end of our single survey reach. We also recorded air temperature and relative humidity ca. 2 m above ground, water temperature, and substrate temperature at the beginning and end of each VES. We used a Kestrel 3500 (Nielsen-Kellerman, Boothwyn, Pennsylvania) to measure air temperature and relative humidity and a Mestek Industrial infrared thermometer (Shenzhen Mestek Tools Co., LTD, Longhua, Shenzhen, China) for all other measurements. We recorded the location of all captured gartersnakes using GPS units (UTM WGS84) and the aforementioned weather measurements at each capture location. If a gartersnake was captured under a cover object, we also took the substrate temperature under that cover object using the infrared thermometer.

Each season, we placed between 35 and 111 Gee® minnow traps (mean = 86) with 3.175 mm mesh and/or Promar collapsible minnow traps with dual 63.5 mm openings and polyethylene mesh (Memphis Net and Twine, Memphis, Tennessee) modified to 25.4 mm openings with felt reducers along the stream bank per session. During 2022, we also tested modified Gee traps wherein we placed a pair of 0.15 m x 0.5 m wire hardware cloth wings to each end of the trap to enlarge the effective opening of the trap as described by Halstead et al. (2013). We placed traps with ~15-m spacing throughout the majority of our survey reach during most survey sessions with some exceptions where the focus of the session was to specifically maximize gartersnake captures in particular areas (Tables 1 & 2). Traps were secured to the bank with cord and stakes, and we ensured there was sufficient space in the trap for air-breathing animals to take air. We placed 20 cm lengths of foam tubing or an empty 0.47-liter water bottle in each trap as a flotation aid. During most survey sessions (Tables 1 & 2), we baited traps with dead rainbow trout from the nearby Canyon Creek Fish Hatchery, however, traps were ‘self-baited’ as live fish entered them and were not removed. We checked traps twice per day and recorded the presence of live fish, anuran tadpoles, and water bugs (Belostomatidae), and we noted if the trout bait was still present. Some traps were raided by raccoon (*Procyon lotor*) which removed traps from the water and/or removed the dead rainbow trout; we removed these traps from effort calculations.

Table 1. Survey and trapping effort and success for *Thamnophis rufipunctatus* (THRU) using visual encounter survey (VES) and aquatic minnow traps at Canyon Creek, Arizona, during 2022–2024. Trip types are: Trap (VES and trapping), Track (sessions focused on radio telemetry monitoring), and Zoo (release of zoo-born THRU). Incidental captures were made outside of formal VES. *Indicates traps were baited with dead rainbow trout from Canyon Creek Fish Hatchery.

Year	**Trip**	**Number of Traps**	**Trap nights**	**Trap hours**	**VES hours**	**VES**	**Trap**	**Incidental**	**THRU Total**	**Cap/ 100 VES hours**	**Cap/ 100 Trap hours**
2022	Trap P1 June (13-15)	81	160	3840	22.6	0	0	1	1	0	0
2022	Trap P2 July (11-13)	107	214	5136	8.8	0	0	0	0	0	0
2022	Trap P3 July (18-21)*	35	85	2040	22.3	1	1	0	2	4.494	0.049
2022	Zoo Y1 August 15	0	NA	NA	22.5	3	0	0	3	13.333	NA
2022	**TOTALS**	223	459	11016	76.2	4	1	1	6	5.251	0.009
2023	Trap 1 May (24-30)*	85	506	12144	67.6	5	5	1	11	7.394	0.041
2023	Track 1 June (6-9)*	50	147	3528	27.9	1	1	1	3	3.584	0.028
2023	Track 2 June (12-15)	0	NA	NA	37.7	3	0	0	3	7.968	NA
2023	Trap 2 June (21-28)*	100	694	16656	84.1	3	9	1	13	3.567	0.054
2023	Trap 3 July (19-26)*	102	687	16488	72.9	1	3	2	6	1.372	0.018
2023	Track 5 August (1-3)	0	NA	NA	6.0	0	0	0	0	0.000	NA
2023	Trap 4 August (16-23)*	108	747	17928	91.6	9	10	4	23	9.825	0.056
2023	**TOTALS**	445	2781	66744	387.8	22	28	9	59	5.673	0.042
2024	Trap 5 May (22-26)	111	479.5	11508	63.3	1	0	0	1	1.579	0.000
2024	Trap 6 June (19-26)*	105	735	17640	73.5	2	4	0	6	2.720	0.023
2024	Trap 7 July (17-20)*	110	385	9240	54.7	0	2	0	2	0.000	0.022
2024	Trap 8 August (19-20)*	40	60	1440	17.4	0	4	3	7	0.000	0.278
	TOTALS	366	1660	39828	208.9	3	10	3	16	1.436	0.025
2022-2024	**Combined TOTALS**	1034	48900	117588	673.9	29	39	13	81	4.310	0.033

Table 2. Survey and trapping effort and success for *Thamnophis elegans* (THEL) using visual encounter survey (VES) and aquatic minnow traps at Canyon Creek, Arizona, during 2022–2024. Trip types are: Trap (VES and trapping), Track (sessions focused on radio telemetry monitoring), and Zoo (release of zoo-born THRU). Incidental captures were made outside of formal VES. *Indicates traps were baited with dead rainbow trout from Canyon Creek Fish Hatchery.

Year	Trip	Number of Traps	Trap nights	Trap hours	VES hours	VES	Trap	Incidental	THEL Total	Cap/100 VES hours	Cap/100 Trap hours
2022	Trap P1 June (13-15)	81	160	3840	22.6	6	2	0	8	26.513	0.052
2022	Trap P2 July (11-13)	107	214	5136	8.8	3	0	0	3	34.091	0.000
2022	Trap P3 July (18-21)*	35	85	2040	22.3	1	3	0	4	4.494	0.147
2022	**TOTALS**	223	459	11016	53.7	10	5	0	15	18.629	0.045
2023	Trap 1 May (24-30)*	85	506	12144	67.6	10	3	2	15	14.789	0.025
2023	Track 1 June (6-9)*	50	147	3528	27.9	8	1	0	9	28.674	0.028
2023	Track 2 June (12-15)	0	NA	NA	37.7	9	0	0	9	23.904	NA
2023	Trap 2 June (21-28)*	100	694	16656	84.1	2	10	7	19	2.378	0.060
2023	Trap 3 July (19-26)*	102	687	16488	72.9	8	14	4	26	10.974	0.085
2023	Track 5 August (1-3)	0	NA	NA	6.0	1	0	0	1	16.576	NA
2023	Trap 4 August (16-23)*	108	747	17928	91.6	5	5	10	20	5.459	0.028
2023	**TOTALS**	445	2781	66744	387.8	43	33	23	99	11.088	0.049
2024	Trap 5 May (22-26)	111	480	11508	63.3	8	4	1	13	12.632	0.035
2024	Trap 6 June (19-26)*	105	735	17640	73.5	5	8	1	14	6.801	0.045
2024	Trap 7 July (17-20)*	110	385	9240	54.7	3	8	1	12	5.482	0.087
2024	Trap 8 August (19-20)*	40	60	1440	17.4	8	0	0	8	46.056	0.000
	TOTALS	366	1660	39828	208.9	24	20	3	47	11.486	0.050
2022-2024	**Combined TOTALS**	1034	4900	117588	650.4	77	58	26	161	11.838	0.0490

We recorded the snout-vent length (SVL), tail length (mm), mass (g, Ohaus digital scale, Parsippany, New Jersey), and sex of all captured gartersnakes. SVL and tail lengths were recorded by gently stretching the gartersnake along a measuring tape, along with noting any traumas to the body of the snake and or tail. We uniquely marked individuals with subcutaneously injected PIT tags, visual implant elastomer (VIE; Major et al. 2020), and/or branding ventral scales (Winne et al. 2006). We used two types of PIT tags during this study; 144 snakes were marked with APT12 tags (12.5 mm l x 2.03 mm d, 134.2 kHz) in 2023–2024) and nine snakes with Biomark HDX12 tags (12 mm l x 2.12 mm, 134.2 kHz) in 2022. Both types of tags applied are readable by universal PIT tag scanners. We collected blood samples from each captured snake by puncturing the caudal vein to obtain a blood dot smear on a Genesaver 2.0 card, or removing ca. 5–9 mm of the tail tip immediately stored in 90% EtOH for future genetic analysis (e.g., Wood et al. 2018).

During a single survey in August 2024, we conducted a preliminary test of PIT tag telemetry during a VES. We used a HPR+ portable reader and HP antenna (Biomark, Boise, Idaho) as described in Oldham et al. (2016) who reported that their use of Biomark HPT12 (12.5 mm, 132.4 kHz) PIT tags had read depth ranges from 30.5 cm to 43.2 cm. A single observer walked within ca. 10 m of the stream edge moving the HP antenna over potential cover objects to scan for PIT-tagged gartersnakes.

Passive PIT Tag Arrays

During 2024, we deployed four passive PIT tag arrays in a preliminary test of these systems to detect PIT-tagged gartersnakes. Each array consisted of a Biomark IS1001 RFID PIT tag reader, a Biomark junction box, and a 15.24 m Biomark cord antenna. We arranged the cord antennas in a loop with each side of the loop separated by 0.15–0.45 m for ca. 7.62 m of coverage. We placed antennas on the stream bank parallel to the stream and 0.5–2 m from the water's edge. Preliminary tests indicated that antennas could detect a 12-mm Biomark APT12/ HDX12 PIT tag within ca. 75 mm. Each array was powered by a Wattcycle (Shenzhen, China) 12-V 100 AH LiFePO – BCI group 24 battery housed within a Polyethylene MEIJIA (Shanghai, China) waterproof portable equipment case. The connection from the battery box to the reader box was made with Thomas Betts LTC050 extra flex liquid tight and Eaton LT10090NMBL or LT100NMBL fittings with galvanized rigid couplings. XHHW 10-gauge stranded copper wire was used from the battery terminals into the reader box and then spliced to MTW 16-gauge wire and connected to the reader board. Each battery provided power for approximately one month. To maximize battery life potential, the Biomark IS1001 readers were programmed to have a 500 ms delay scan pulse (default 120 ms) and standby time from 23:00 hr to 05:00 hr (unable to scan/minimal power draw). We also set the unique function to 'delay' with a 60-sec timer which allowed an individual to only be scanned every 60 sec of time in contact with the antenna instead of every scan pulse. All connections and settings/firmware updates and downloading of data were made using Biomark Device Manager software (v.1.2.37). Because this was, to our knowledge, the first application of using passive PIT tag arrays for monitoring semiaquatic snakes, we placed our four arrays in areas that we thought would maximize detections of PIT-tagged snakes to confirm that wild snakes could be detected. We therefore selected four locations within our survey reach where most of our 2023 gartersnake captures had occurred. We downloaded data from each array and changed batteries periodically between 14 May and 3 October 2024 (Table 3).

Table 3. Detections of *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) by four passive PIT tag arrays at Canyon Creek, Arizona, during 2024. Hours deployed are the cumulative number of hours during each period that arrays were on and scanning for PIT-tagged snakes. Trap refers to formal survey sessions using visual encounter surveys and trapping. Contacts represent the total number of contacts by PIT-tagged snakes across all four units. Unique represents the number of uniquely marked individual snakes detected per trip. THRU/THEL Unique columns represent unique snakes marked within that period and *Represents the total number of uniquely marked individual snakes detected by passive PIT tag arrays during 2024.

Year	**Period**	**Cumulative Hours Deployed**	**THRU Contacts**	**THRU Unique**	**THRU/ 100 hours**	**THEL Contacts**	**THEL Unique**	**THEL/ 100 hours**
2024	Ant 1 May (14-21)	434	1	1	0.23	1	1	0.23
2024	Trap 5 May (22-26)	358	0	0	0	0	0	0
2024	Ant 2 May 27 - June 18	1642	8	4	0.487	2	1	0.122
2024	Trap 6 June (19-26)	572	0	0	0	3	3	0.524
2024	Ant 3 June 27 - July 16	1455	2	2	0.137	0	0	0
2024	Trap 7 July (17-20)	269	0	0	0	0	0	0
2024	Ant 4 July 21 - August 18	1699	5	4	0.294	0	0	0
2024	Trap 8 August (19-20)	148	0	0	0	0	0	0
2024	Ant 5 August 21 - September 5	1152	5	4	0.434	0	0	0
2024	Ant 6 September (6-20)	1065	2	2	0.188	2	2	0.188
2024	Ant 7 September 21 - October 3	1010	2	1	0.198	3	2	0.297
	TOTALS	9804	25	10*	0.255	11	7*	0.112

Radio Telemetry

We attached VHF temperature-sensitive radio transmitters (PD-2T 2.5 g and BD-2T 1.8 g, Holohil, Carp, Ontario, Canada) externally to select gartersnakes. Transmitters were ≤ 5% of the snake's body weight and did not exceed the snake's body diameter. We followed the general approach described in Wylie et al. (2011) by placing the transmitter on the snake's ventral surface ca. ¾ of the SVL towards the vent with the whip antenna facing posteriorly. We secured transmitters using tape and tried different types and brands of duct and surgical tape during the study. All telemetered gartersnake were released within 24 hours of capture at their original site of capture. We used Telonics TR-8 (Mesa, Arizona) handheld receiver along with ATS 3 element folding Yagi antenna (Advanced Telemetry Systems Inc., Isanti, Minnesota) to locate telemetered snakes.

We located telemetered snakes every 1–2 days during each of our four survey session during 2023. We also made four additional trips to our study area of 1–4 days in length between our main trapping trips to collect additional telemetry data in 2023 (hereafter tracking sessions). We typically located telemetered snakes once per day but located individuals two or three times per day when time permitted. We recorded each telemetered snake's location, time, and weather data as described above. We also recorded the transmitter's pulse rate as the number of pulses per minute as reported on the TR-8 receiver. Finally, we recorded a brief description of the snake's environment, whether the snake was visible or seen with the transmitter still attached, and any observed behavior.

Analysis

Because we used three different methods for capturing and/or detecting gartersnakes, we calculated catch-per-unit-effort (CPUE) separately for each method. We calculated VES CPUE as the number of gartersnakes captured per survey session divided by the number of person-hours during that session and standardized to captures per 100 person-hrs. We calculated a total VES CPUE as the total number of captures across the study divided by the total number of person-hours and standardized to captures per 100 person-hrs. We did not include 'incidental' gartersnakes captured outside of formal VES (e.g., while setting/removing/checking traps) in these calculations. We calculated trapping CPUE as the number of gartersnakes captured in traps during each trip divided by the number of trap-hrs for that trap and standardized to trap captures per 100 trap-hrs. We calculated a total trapping CPUE as described above for VES CPUE. Finally, we calculate a CPUE from the passive PIT tag arrays as the number of individual PIT tagged snake contacts by each array during each array sampling session. We defined contacts as the PIT antennas registering a PIT tag from a snake, but did not include multiple instances of contacts for the same individual within a short time period (e.g., not more than one contact per equivalent VES/trap check), which led to only including one contact per antenna-day. We then calculated a total CPUE from PIT tag arrays as the number of gartersnake contacts divided by the total number of hours all arrays were deployed and scanning during a given array sampling session, which we then standardized to contacts per 100 antenna-hrs. We compared CPUE between VES and trapping for each session using paired Wilcoxon signed rank tests in Program R (v. 4.4.1, R Core Team 2024) to account for data that were nonnormally distributed. We used t-tests to compare CPUE between sessions using trapping and sessions using passive PIT tag arrays for THRU and for THEL.

We evaluated changes in body size (SVL and weight) between consecutive recaptures between male and female gartersnakes and between THRU and THEL using generalized linear mixed models (GLMM). Because our response variable (change in SVL or weight) was continuous and could be negative we used a GLMM with a Gaussian error distribution and identity link. We included sex and species as additive effects in each model. To control for variation in the time between consecutive recaptures among individuals, we included the number of days between consecutive captures in all models as a continuous fixed effect covariate. Smaller individuals may also show a greater change in body size due to faster growth rates by younger individuals. We therefore also included an individual's size (SVL or weight) at its first capture as a continuous fixed effect covariate in our model to control for initial body size. Because we had multiple measurements from the same individuals, we used random intercepts for individuals to account for non-independence of multiple observations from the same individual. We fit all GLMM using the glmmTMB package (Brooks et al. 2017).

To evaluate gartersnake movement patterns and the extent to which those patterns may differ between THRU and THEL, we first measured the Euclidean distance between consecutive gartersnake captures (both physical captures and PIT tag array detections). We were also interested in whether individuals were more likely to move greater distances when moving downstream (i.e., with the stream flow). Because our survey reach flowed predominately northwest to southeast, we recorded whether a recapture was north (upstream) or south (downstream) of each gartersnakes previous capture point. We then evaluated the effects of sex, species (THRU and THEL), and direction of movement on distance between recaptures using a GLMM. To account for the right-skew of our continuous, positive-only data we used a gamma error distribution with a log link. Our model included an interactive effect between species and the downstream covariate and an additive effect of sex. We again included the number of days between consecutive captures to control for varying durations between recaptures and random intercepts for individuals to control for multiple measurements from the same individuals.

We modeled change in SVL using a von Bertalanffy growth model (Fabens 1965) that accounts for individual heterogeneity in growth rates and measurement error (Eaton and Link 2011; Rose et al. 2018a; Chandler et al. 2023). This model includes three parameters, asymptotic body size (Linf), rate at which size approaches the asymptotic size (k), and the ratio of the mean to the variance for the gamma distribution that is used to model the growth increments for each individual and thereby account for individual heterogeneity in growth rates (lambda). This model treats the true SVL as an unobserved latent parameter and uses a stochastic gamma process to model measurement error (Eaton and Link 2011). We modeled each parameter (Linf, k, and lambda) as an additive function of species (THEL vs. THRU) and sex. Two THRU neonates (THRU10, THRU13) did not have SVL measurements on their initial capture in August 2022 but were both recaptured during 2023. To incorporate information from these individuals in the growth model we assigned their initial SVL as the mean SVL across the 12 other neonatal THRU that we captured during surveys in August of 2023 and 2024. We fit this model using a Bayesian approach. We constricted prior distributions (Table 4) as necessary to ensure sufficient model convergence (c.f., Rose et al. 2018*a*, Chandler et al. 2023) while ensuring that our inferences were not sensitive to our choice of priors. Two individuals (both THEL) had unrecorded sex so we interpolated their sex using Bernoulli sample with the proportion of males estimated from our data with a Beta prior with shape parameters = 1. We fit our growth model in R (v4.4.1) using JAGS (Plummer 2003) and the jagUI package (Kellner 2015). We fit our growth models using 25,000 adaptive iterations and 50,000 burn-in iterations followed by 200,000 iterations and we retained every 10th posterior draw from 4 parallel chains. We examined trace plots to confirm appropriate levels of mixing. All Gelman-Rubin statistics ($\hat{R}$) were ≤ 1.005 for all model parameters (Brooks and Gelman 1998; Gelman and Hill 2006). We report posterior means, 95% credible intervals (CRI; 2.5th and 97.5th quantiles), and posterior probabilities (PP), which we calculated as the proportion of posterior samples that had the same sign as the posterior mean and which ranged from 0.5–1.0.

We used a Cormack-Jolly-Seber (CJS) model to estimate apparent survival (φ) and recapture probabilities (p) for THRU and THEL (Cormack 1964; Jolly 1965; Seber 1965); we did not have enough captures to include THCY. One of the limitations of the CJS model is that it cannot distinguish between true survival and permanent emigration. Apparent survival rates may therefore underestimate true survival rates. We modeled annual apparent survival as an additive function of species and SVL. To account for potential changes in SVL during our study, particularly for smaller sized individuals that could have increased their SVL during our study, we used our Von Bertalanffy growth model to predict SVL for each individual at every capture occasion, which allowed us to treat SVL as a time-varying individual covariate. We did not include sex as a covariate in our final model because preliminary analyses indicated no differences in apparent survival between males and females. To evaluate differences in sampling method efficacy for each species, we first modeled recapture probability as an interaction between species and three types of sampling sessions. The first type of session is what we refer to as Surveys, which included VES and trapping. We included trapping sessions during 2024 where passive PIT tag arrays were deployed because preliminary analyses indicated no differences in recapture probability between these sessions and survey sessions without passive PIT tag arrays. The second type of session is what we refer to as Antenna, which were sessions during 2024 where only passive PIT tag arrays were deployed. Because some individuals (e.g., neonates marked during 2023 with VIE) did not have PIT tags during 2024 and therefore could not be detected with passive PIT tag arrays, we fixed recapture probability to zero for these individuals during the antenna sessions. The third type of session is what we refer to as Other, which includes sessions other than our formal survey sessions (e.g., trips focused on radio telemetry, releases of zoo-born THRU by project collaborators at the Phoenix Zoo). We estimated a constant recapture probability during Other sessions across species. Finally, we also modeled recapture probability using an additive effect of SVL during Survey sessions because we assumed that a PIT tagged individual's probability of being detected on a passive PIT tag array was independent of body size. We used vague priors for most parameters, including a Gaussian prior with mean = 0 and SD = 1.6485 for the slopes of SVL. We estimated group-specific probabilities as intercepts on the probability scale using Beta priors with shape parameters = 1 with the exception of annual apparent survival for THEL where we used a Gaussian prior (mean = 0.14, SD = 0.25) truncated between 0.0001 and 0.9999 to facilitate convergence due to relatively low recapture rates for THEL. We fit models using 25,000 adaptive iterations and 25,000 burn-in iterations followed by 125,000 iterations and we retained every 10th posterior draw from 4 parallel chains. We examined trace plots to confirm appropriate levels of mixing. All Gelman-Rubin statistics ($\hat{R}$) were ≤ 1.058 for all model parameters (Brooks and Gelman 1998; Gelman and Hill 2006).

We used a Jolly-Seber (JS) model to estimate THRU abundance (Jolly 1965; Seber 1965). The JS model uses an open-population format similar to the CJS model except that the JS also estimates abundance (N) for each capture occasion in addition to apparent survival (φ) and recapture probabilities (p). The JS model assumes that all individuals in the population, both marked and unmarked individuals, have the same capture probability (Williams et al. 2002). We therefore only used recaptures of THRU made during VES and trapping and excluded recaptures made using passive PIT tag arrays and PIT-tag telemetry because these latter two methods are applicable only to previously marked individuals. Although we have no reason to suspect that capture probabilities differ between marked and unmarked THRU in our study area, any behavioral response to capture (e.g., by marked individuals becoming more secretive as a negative response to capture and handling) would bias abundance estimates. We therefore caution that inferences made using these abundance estimates rely on the validity of our model assumptions. We did not explore closed-population models for estimating abundance because of the sparsity of recaptures made using only VES and trapping. We fit a JS model using the restricted occupancy model parameterization that treats super-population size (N_{Super}) as a derived parameter (Kery and Schaub 2012). This formulation estimates a probability of recruitment (γ) which is the probability that an individual in N_{Super} will be captured and marked (i.e., “recruited” into the study population). We estimated a constant term for apparent survival and recruitment probability using vague Beta priors with shape parameters = 1. We followed a similar model structure for recapture probability as we did for our CJS survival model wherein we allowed recapture probability to vary between the two types of sampling sessions represented in our JS data (i.e., Survey and Other). We estimated session-specific probabilities as intercepts on the probability scale using Beta priors with shape parameters = 1. Because of the low numbers of individuals used in the JS analysis (n = 58) and the low numbers of recaptures (11 of the 58 individuals recaptured on a single subsequent sampling session), we explored different parameterizations for recruitment probability. We fit two JS models, one with recapture probability held constant and another where it was allowed to vary between our two types of sampling sessions. We used the same Beta priors as for all other model parameters. Finally, we calculated an additional derived parameter, mean N, by averaging the estimates of N for each survey session. We fit models using 25,000 adaptive iterations and 25,000 burn-in iterations followed by 225,000 iterations and we retained every 10th posterior draw from 4 parallel chains. We examined trace plots to confirm appropriate levels of mixing. All Gelman-Rubin statistics ($\hat{R}$) were ≤ 1.052 for all model parameters (Brooks and Gelman 1998; Gelman and Hill 2006).

Results

Surveys Summary

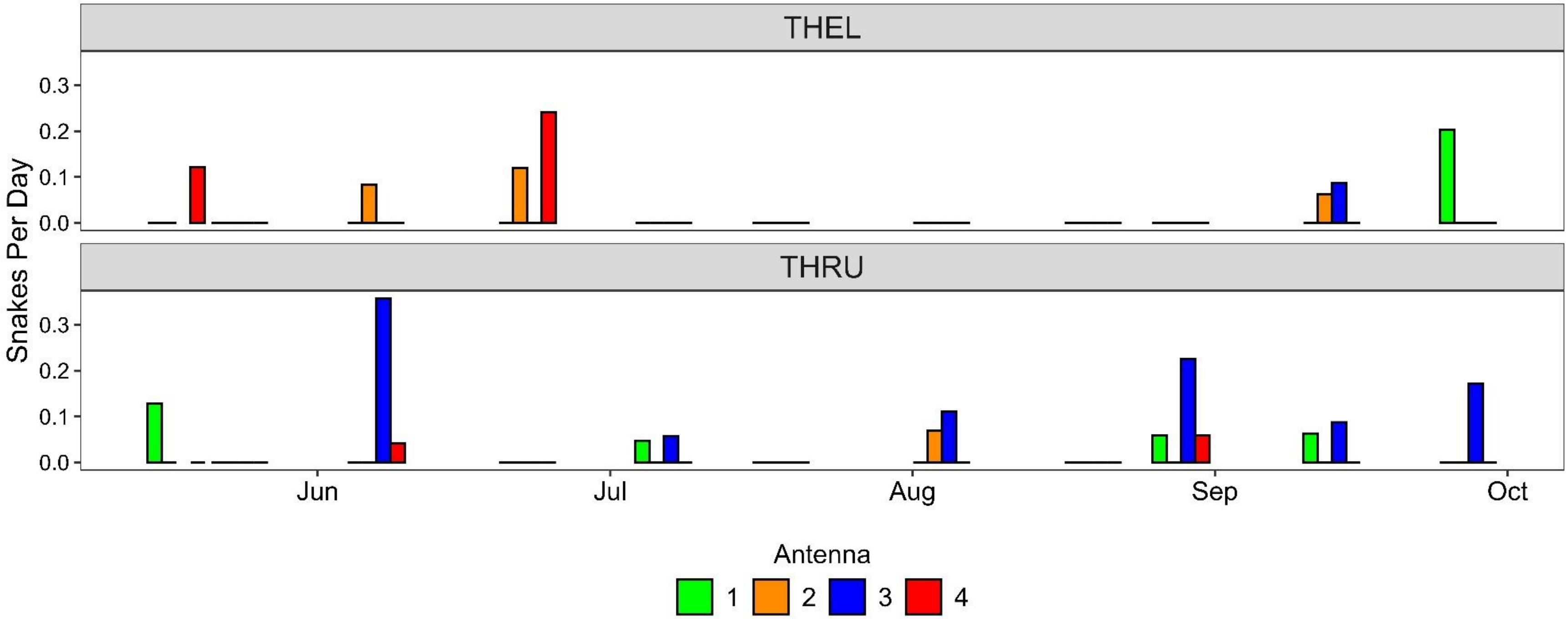
During our 15 different survey sessions, we captured and marked 61 THRU with a total of 81 captures (Table 1), marked 131 THEL with a total of 161 captures (Table 2), and marked 8 THCY with a total of 9 captures (two neonates, six juveniles/adults). Trap-hrs per session ranged from zero (Track/Release trips) to 17,928 (mean = 8,399 trap-hrs; SD = 6,902), while VES-hours per session ranged from 6.03 to 91.60 (mean = 46.46 VES-hrs; SD = 29.30). CPUE for both species varied markedly among sessions, years, and species. There was evidence that VES was more effective than trapping for both THRU (mean = 3.04 captures per 100 person-hrs; SD = 3.12; mean = 0.05 captures per 100 trap-hours; SD = 0.08; V=52, $P = 0.014$) and THEL (mean = 17.06 captures per 100 person-hrs; SD = 13.04; mean = 0.05 captures per 100 trap-hours; SD = 0.04; V = 78, $P = 0.001$). VES captures per 100 person-hrs were higher for THEL (mean = 17.06 captures per 100 person-hrs; SD = 13.04) than THRU (mean = 3.04 captures per 100 person-hrs; SD = 3.12; V = 4, $P = 0.004$). We did not find evidence that trap capture rates differed between THEL (mean = 0.05 captures per 100 trap-hours; SD = 0.04) and THRU (mean = 0.05 captures per 100 trap-hours; SD = 0.08; V = 16, $P = 0.262$). We did not capture neonatal THRU before

August in any year, whereas we captured neonatal THEL as early as 20 June through 20 August. Peak captures of THRU occurred during August in each year, which reflected the presence of neonates, although the greatest number of captures occurred during either June or July sessions for THEL (Tables 1 & 2).

Survey Method Comparison

We had 25 contacts from 10 PIT tagged THRU and 11 contacts from seven PIT tagged THEL across all four passive PIT tag arrays during 11 sampling periods between mid-May and early October (Table 3). Contacts per 100-hrs of deployment (i.e., PIT tag array CPUE) varied both among antenna arrays and over the 2024 sampling season for both species (Figure 2). There was no evidence that CPUE for passive PIT-tag arrays differed between tagged THRU (mean = 0.18 contacts per 100 antenna-hrs; SD = 0.17) and THEL (mean = 0.12 contacts per 100 antenna-hrs; SD = 0.17; t = 0.745, df = 19.996, *P* = 0.465). We also found no evidence that tagged THEL CPUE differed between trapping (mean = 0.05 captures per 100 trap-hours; SD = 0.04) or the passive PIT tag arrays (mean = 0.12 captures per antenna-hours; SD = 0.17; t = 1.394, df = 11.061, *P* = 0.191). However, the passive PIT tag arrays had higher CPUE for THRU (mean = 0.18 captures per 100 antenna-hours; SD = 0.17) compared to trapping (mean = 0.05 captures per 100 trap-hours; SD = 0.08; t = 2.304, df = 13.345, *P* = 0.038).

Figure 2. Detections of *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) by four passive PIT-tag arrays at Canyon Creek, Arizona, during 2024. Detections are standardized to the number of contacts per ‘day’ which consisted of antennas scanning from 05:00–23:00 (Outside this period they were in stand-by mode to conserve battery).



Growth Rate

We obtained 18 measurements of change (Δ) in SVL from 16 gartersnakes (11 THEL and five THRU). Number of days between consecutive recaptures ranged from 23 to 378 days (median = 73 days) and SVL at first capture ranged from 202 to 536 mm (median = 417 mm). Although THRU had greater changes in SVL between consecutive recaptures (mean Δ = 77.60 mm, SD = 86.13) than THEL (mean Δ = 25.92 mm, SD = 31.81), after controlling for initial body size and time between consecutive recaptures we did not find evidence of differences in change in SVL between consecutive recaptures between THRU and THEL ($\beta_{\text{THRU}} = 28.02$, $P = 0.167$). We found evidence that gartersnakes captured at larger SVL had less change in SVL between consecutive recaptures ($\beta_{\text{First\_SVL}} = -0.21$, $P = 0.014$) and that SVL of males changed less (mean Δ = 20.73 mm, SD = 28.62) than females (mean Δ = 71.00 mm, SD = 73.55; $\beta_{\text{Male}} = -31.42$, $P = 0.044$). We also found a strong positive effect of time since previous recapture on change in SVL ($\beta_{\Delta\text{Time}} = 0.13$, $P = 0.008$).

We obtained 19 measurements of change in weight from 17 gartersnakes (10 THEL and 7 THRU). Number of days between consecutive recaptures ranged from 14 to 378 days (median = 56 days) and weight at first capture ranged from 4 to 88 g (median = 38 g). We did not find evidence of differences in change in weight between consecutive recaptures between THRU (mean = Δ9.29 g, SD = 12.56) and THEL (mean = Δ8.42 g, SD = 12.30; $\beta_{\text{THRU}} = -4.55$, $P = 0.438$) after controlling for initial body weight and time between consecutive recaptures. Changes in body weight were also similar between sexes (Males: mean = Δ6.36, SD = 7.70; Females: mean = Δ12.00, SD = 16.35; $\beta_{\text{Male}} = -5.27$, $P = 0.275$). Time since last recapture had little effect on change in body weight ($\beta_{\Delta\text{Time}} = -0.002$, $P = 0.880$). We also found that gartersnakes initially captured at larger weights had less change in weight between consecutive recaptures (β_{First_Weight} = -0.22, *P* = 0.044).

We used SVL measurements from 191 individuals (57 THRU and 134 THEL) to fit our von Berttalanffy growth model. We had 8 individual THRU and 12 individual THEL with more than one SVL measurement. Number of days between recaptures ranged from 23 to 378 days (median = 287 days). Our growth model indicated no strong evidence of variation between species or sex for asymptotic length, growth rate, or individual heterogeneity in growth rate with the posterior probabilities for all coefficient parameters being ≤ 0.78 (Table 4). The strongest effect was for higher individual heterogeneity in growth rate for males compared to females (λ_{MALE} = 164.98, 95% CRI = 139.50–650.40, PP = 0.78).

Table 4. Model parameters, prior distributions, and posterior means (Mean), quantile-based 95% credible interval (CRI), and posterior probabilities (PP) from a Von Bertalanffy growth model fit to snout vent length data from *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) at Canyon Creek, Arizona, during 2022–2024. The posterior probability represents the proportion of posterior samples that have the same sign as the posterior mean.

Parameter	**Covariate**	**Prior**	**Mean**	**LCRI**	**UCRI**	**PP**
Asymptotic length	Linf	Normal(0.80,0.289)T(0,)	0.617	0.419	0.84	1
Asymptotic length	Linf(THRU)	Normal(0,0.316)	0.068	-0.198	0.399	0.667
Asymptotic length	Linf(Male)	Normal(0,0.316)	-0.058	-0.275	0.177	0.725
Annual growth rate	k	Normal(1,0.316)T(0,)	1.029	0.523	1.568	1
Annual growth rate	k(THRU)	Normal(0,0.316)	-0.018	-0.534	0.529	0.535
Annual growth rate	k(Male)	Normal(0,0.316)	0.144	-0.433	0.729	0.684
Individual variation	lambda	Normal(150,100)	160.217	36.604	323.532	1
Individual variation	lambda(THRU)	Normal(0,100)	-18.715	-167.157	148.112	0.612
Individual variation	lambda(Male)	Normal(0,316.228)	164.977	-139.497	650.397	0.779
Measurement error	sd.eps	Uniform(0,0.5)	0.02	0.012	0.031	1

Movement

We attached external VHF transmitters to 6 THRU, 10 THEL and 1 THCY and found that transmitters generally came off the snakes in less than 2 weeks, although in 6 cases (one THRU, five THEL) within 24 hrs after attachment (Table 5). Excluding the six cases of attachment failure, tracking duration of THRU ranged from 9–12 days (mean = 10.2 days; SD = 0.7; *N* = 4 males, 1 female), THEL from 2–42 days (mean = 18.4 days SD = 6.7; *N* = 1 male, 4 females), and THCY 4 days (1 female). Due to small sample sizes and single female and male tracked for THRU and THEL respectively, we did not compare movements between sexes. Cumulative distance moved ranged from 18.53–94.09 m for THRU (mean = 51.6 m; SD = 24.43), 24.09–119.46 m for THEL (mean = 67.69 m; SD = 35.37), and 43.7 m for THCY (Table 1.5). We recorded a total of 30 locations for THRU, 43 for THEL, and 5 for THCY, and found all three species remained relatively close to the stream. The farthest distance THRU moved from the stream was 34 m by a female on 8 June 2023, whereas one female THEL and THCY moved 50 m from the stream on 2 September 2023 and 23 August 2023, respectively. We encountered unexpected problems with the tape attachment method that resulted in snakes experiencing a skin reaction presumably from the tape’s adhesive or other issues. Out of an abundance of caution for the snake’s wellbeing, we removed all the transmitters and ceased further telemetry.

Table 5. Summary of radio telemetry data collected using externally attached VHF transmitters on *Thamnophis rufipunctatus* (THRU), *T. elegans* (THEL), and *T. cyrtopsis* (THCY) at Canyon Creek, Arizona, during 2023. Snake ID represents a unique individual by species. Cumulative distance is the cumulative Euclidian distance between each consecutive telemetry location, and max DTW is the maximum Euclidean distance from water across each individual's telemetry locations. All THRU transmitters were removed 8 June 2023 due to complications from external transmitter attachment.

Snake ID	**Start Date**	**End Date**	**Sex**	**Mass (g)**	**SVL (mm)**	**Number of Locations**	**Total Days Tracked**	**Cumulative Distance**	**Max DTW (m)**
THRU2	27-May-23	8-Jun-23	Male	58	454	9	12	54.58	20
THRU3	27-May-23	8-Jun-23	Male	50	443	7	12	94.09	12
THRU6	28-May-23	6-Jun-23	Male	68	511	3	9	45.74	10
THRU8	30-May-23	8-Jun-23	Female	53	491	5	9	45.04	34
THRU9	30-May-23	8-Jun-23	Male	49	494	6	9	18.53	10
THRU14	8-Jun-23	8-Jun-23	Female	114	567	1	0	NA	1
THEL20	12-Jun-23	12-Jun-23	Male	51	463	1	0	NA	1
THEL21	12-Jun-23	5-Jul-23	Female	96	507	11	23	80.77	45
THEL31	14-Jun-23	15-Jun-23	Male	67	506	3	1	24.09	3
THEL34	21-Jun-23	23-Jun-23	Female	72	484	3	2	42.71	14
THEL49	5-Jul-23	5-Jul-23	Female	96	526	1	0	NA	0
THEL57	22-Jul-23	2-Sep-23	Female	88	520	16	42	119.46	50
THEL60	22-Jul-23	22-Jul-23	Male	43	489	1	0	NA	0
THEL62	22-Jul-23	2-Aug-23	Male	46	474	7	11	102.12	16
THEL79	20-Aug-23	20-Aug-23	Male	71	513	1	0	NA	0
THEL80	19-Aug-23	2-Sep-23	Female	47	459	6	14	36.97	20
THCY2	19-Aug-23	23-Aug-23	Female	92	631	5	4	43.7	50

We had 61 measurements of Euclidean distance between consecutive recaptures across 41 individuals (22 THRU and 19 THEL). Distances ranged from 1 to 813 m (median = 51 m) and the number of days between consecutive recaptures ranged from 0 to 711 days (median = 55 days). More movements were made upstream than downstream (35 and 26, respectively) but this ratio was not significantly different from 1:1 (χ^2 goodness of fit = 1.33, $P = 0.249$). THEL tended to make longer movements downstream (median = 198 m, range = 10–813 m) than upstream (median = 59 m, range = 1–657 m) whereas THRU tended to make shorter movements downstream (median = 23 m, range = 3–151 m) than upstream (median = 42 m, range = 9–602 m). These patterns held true after controlling for time between recaptures as our model showed evidence of shorter downstream movements for THRU ($\beta_{\text{THRU:Downstream}} = -1.53$, $P = 0.022$) along with some evidence of longer downstream movements by THEL ($\beta_{\text{Downstream}} = 0.81$, $P = 0.083$). The main effect of species did now show any evidence of a difference ($\beta_{\text{THRU}} = 0.04$, $P = 0.926$). These results indicated that THRU made generally shorter movements downstream whereas THEL made markedly longer movements downstream (Fig. 3). Cumulative distance moved between recaptures varied for both species, with the longest overall movement at over 813 m by THEL and 602 m by THRU (Fig. 4).

Figure 3. Predicted value of distances moved in meters upstream or downstream with 95% CI for *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) captured at Canyon Creek, Arizona between 2022–2024.

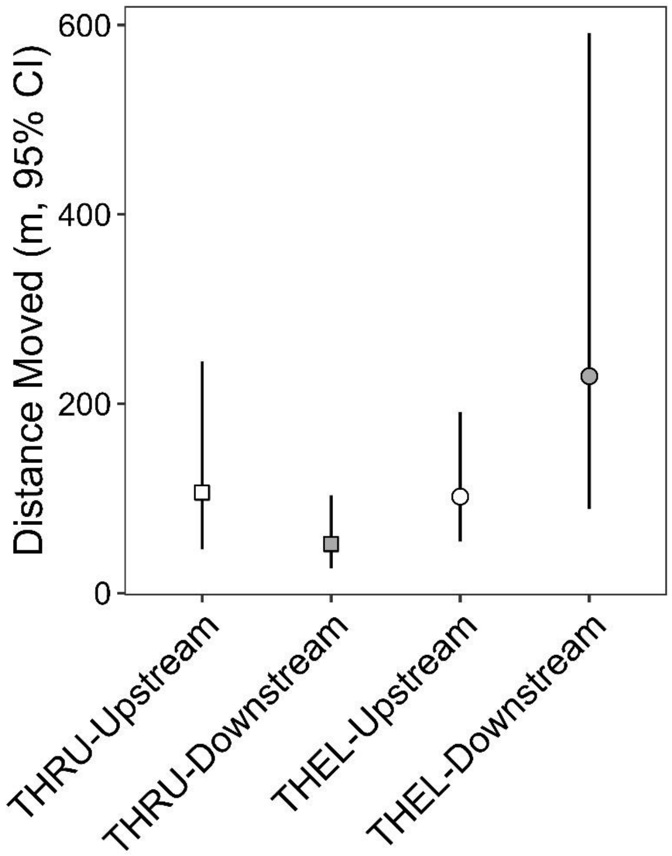
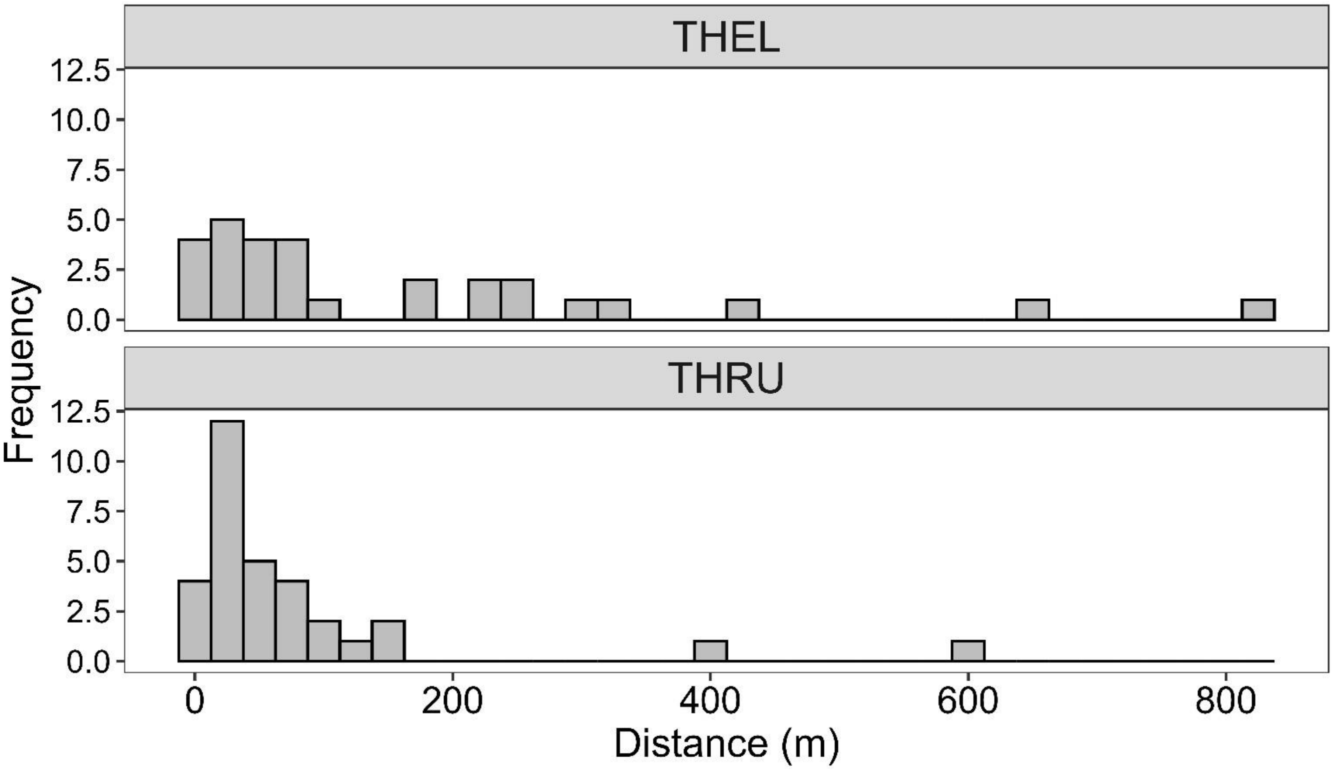


Figure 4. Histogram of Euclidean distances (m) between consecutive recaptures for *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) at Canyon Creek, Arizona during 2022–2024.



Survival

We used mark-recapture data from 58 THRU (27 males and 31 females) and 135 THEL (76 males, 57 females, and 2 of unknown sex). For individuals recaptured in at least one session (18 THRU and 17 THEL), the median number of sessions with a recapture was two for THRU (maximum = six) and two for THEL (maximum = four). Recapture probabilities during VES and trap sessions were similarly low between THRU and THEL ($p < 0.07$, Table 6), however, recapture probabilities during sessions using only passive PIT tag arrays were much higher for THRU ($p = 0.21$, 95% CRI = 0.11–0.34) than for THEL ($p = 0.03$, 95% CRI = 0.01–0.05; Table 6). There was little evidence that SVL influenced recapture probabilities during survey sessions ($\beta = 0.13$, 95% CRI = -0.33–0.60, PP = 0.72) or that SVL influenced annual apparent survival (β

= 0.18, 95% CRI -0.43–0.82, PP = 0.73). Annual apparent survival estimates for an average-size individual were similar between species (THRU: φ = 0.30, 95% CRI = 0.15–0.52; THEL: φ = 0.35, 95% CRI = 0.16–0.62; Table 6).

Abundance

Both JS models for THRU abundance showed satisfactory model convergence (γ(.): max. $\hat{R}$ = 1.052; γ(Survey): max. $\hat{R}$ = 1.028) although we had slightly higher effective sample sizes for most model parameters with the γ(Survey) model (median n. eff = 12,806) than with the γ(.) model (median n. eff = 11,396). Mean *N* for the γ(.) model was 61 (95% CRI = 35–108) and mean N for the γ(Survey) model was 45 (95% CRI = 31–69). Abundance estimates for both models varied across sampling sessions but both indicated an increase in abundance during 2022 (Trap P1-P3 and Zoo Y1), generally higher abundance in 2023 (Trap 1-Trap 4), and lower but more stable abundance in 2024 (Zoo H2-Trap 8; Figure 5). Recruitment probability for the γ(.) model was 0.16 (95% CRI = 0.08–0.29; Table 7). Recruitment probability for Survey sessions was 0.03 (95% CRI = 0.01–0.07) while recruitment probability for Other sessions was 0.16 (95% CRI = 0.08–0.29; Table 7).

Both JS models for THEL abundance showed satisfactory model convergence (γ(.): max. $\hat{R}$ = 1.084; γ(Survey): max. $\hat{R}$ = 1.012) although we had slightly higher effective sample sizes for most model parameters with the γ(Survey) model (median n. eff = 5,836) than with the γ(.) model (median n. eff = 4,693). Mean *N* for the γ(.) model was 248 (95% CRI = 171–330) and mean N for the γ(Survey) model was 199 (95% CRI = 146–281). Abundance estimates for both models varied across sampling sessions but both indicated an increase in abundance during 2022 (Trap P1-P3 and Zoo Y1), generally higher abundance in 2023 (Trap 1-Trap 4), and lower but more stable abundance in 2024 (Zoo H2-Trap 8; Figure 6). Recruitment probability for the

$\gamma(.)$ model was 0.25 (95% CRI = 0.15–0.40; Table 8). Recruitment probability for Survey sessions was 0.11 (95% CRI = 0.05–0.22) while recruitment probability for Other sessions was 0.55 (95% CRI = 0.31–0.86; Table 8).

Table 6. Model parameters, prior distributions, and posterior means (Mean), quantile-based 95% credible interval (CRI), and posterior probabilities (PP) from a Cormack-Jolly-Seber survival model fit using mark-recapture data from *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) at Canyon Creek, Arizona, during 2022–2024. Model parameters include recapture probability (*p*) and annual apparent survival (φ). Surveys are sessions using both VES and trapping while Antenna are sessions where only passive PIT tag arrays were deployed. Other Session includes tracking or release sessions and were pooled across species. β(SVL) is the slope estimate for an additive effect of SVL as a time-varying individual covariate for both *p* and φ predicted from a von Bertalanffy growth model. The posterior probability represents the proportion of posterior samples that have the same sign as the posterior mean.

Parameter	**Covariate**	**Prior**	**Mean**	**LCRI**	**UCRI**	**PP**
Recapture	THEL Surveys	Beta (1,1)	0.051	0.027	0.084	1.000
Recapture	THRU Surveys	Beta (1,1)	0.065	0.028	0.120	1.000
Recapture	THEL Antenna	Beta (1,1)	0.027	0.010	0.053	1.000
Recapture	THRU Antenna	Beta (1,1)	0.211	0.106	0.339	1.000
Recapture	Other Session	Beta (1,1)	0.026	0.009	0.053	1.000
Recapture	β(SVL)	Normal (0,1.648)	0.134	-0.328	0.595	0.716
Survival	THEL φ	Normal (0.4,0.250)T(0.0001,0.9999)	0.350	0.163	0.618	1.000
Survival	THRU φ	Beta (1,1)	0.304	0.147	0.516	1.000
Survival	β(SVL)	Normal (0,1.648)	0.183	-0.433	0.815	0.726

Figure 5. Sampling trip-specific abundance estimates and 95% credible intervals (CRI) *Thamnophis rufipunctatus* (THRU) at Canyon Creek, Arizona during 2022–2024 for models assuming constant recruitment probability (Gamma(.)) and recruitment probability varying between Survey and Other sampling trips (Gamma(Survey)). Solid and dashed dark gray lines represent the mean and 95% CRI, respectively, abundance estimate across all sampling trips for the Gamma(.) model and the solid and dashed light gray lines represent the mean and 95% CRI, respectively, abundance estimates across all sampling trips for the Gamma(Survey) model.

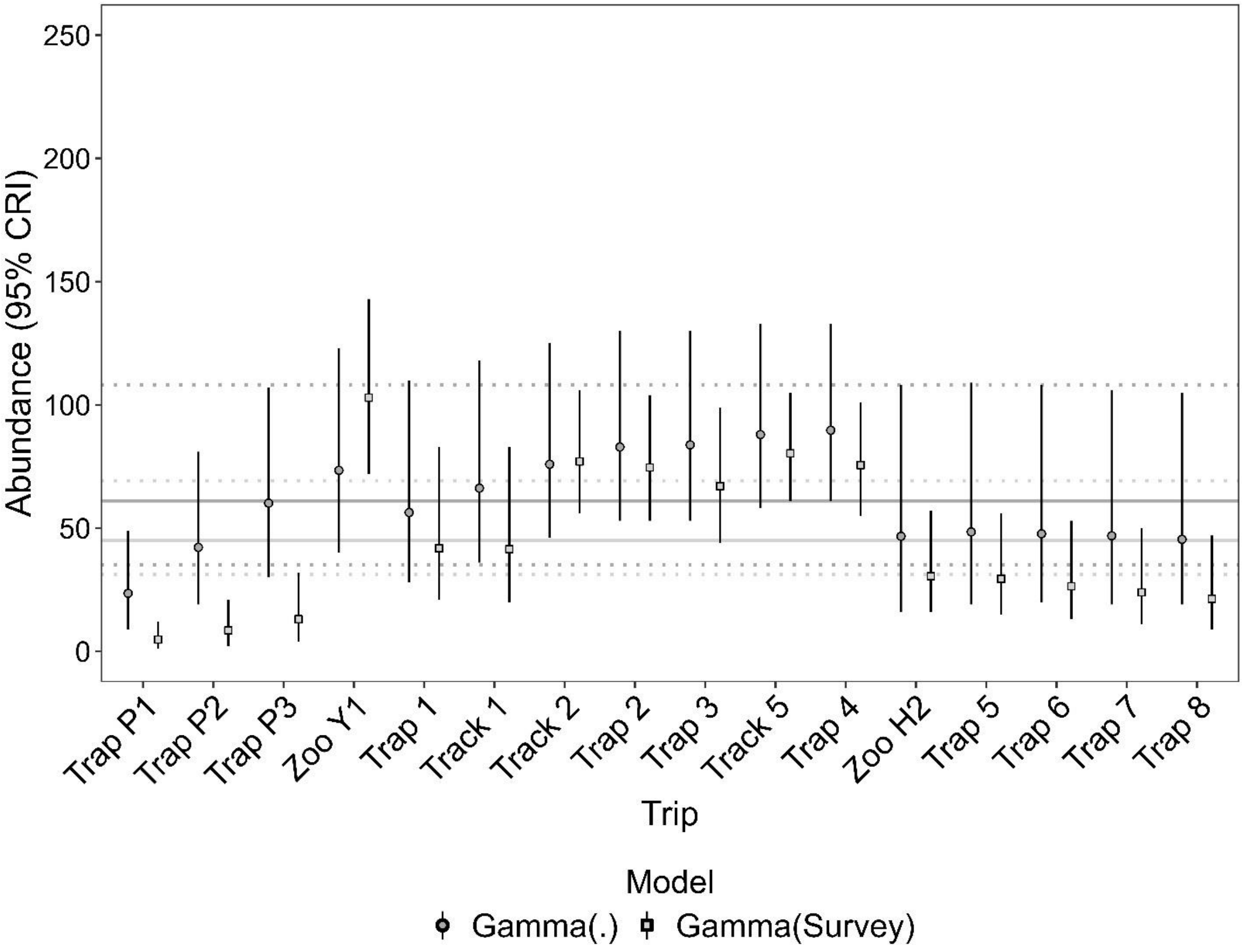


Table 7. Model parameters, prior distributions, and posterior means (Mean) and quantile-based 95% credible interval (CRI) from a Jolly-Seber survival model fit using mark-recapture data from *Thamnophis rufipunctatus* (THRU) at Canyon Creek, Arizona, during 2022–2024. Model parameters include recapture probability (p), annual apparent survival (φ), and recruitment probability (γ). Abundance (N) is estimated as a derived parameter. Surveys are sessions using both VES and trapping and Other are sessions including tracking or release sessions. Super population size (N_{Super}) represents the estimated total number of individuals entering the study population during the study period. Mean abundance (N_{Mean}) is the average abundance estimate across all sampling occasions. Results are presented for models assuming constant γ (γ(.)) and allowing γ to vary between Surveys and Other (γ(Survey)).

Model	**Parameter**	**Prior**	**Mean**	**LCRI**	**UCRI**
γ(.)	Recapture (Survey)	Beta (1,1)	0.10	0.05	0.17
	Recapture (Other)	Beta (1,1)	0.03	0.01	0.06
	Apparent survival	Beta (1,1)	0.39	0.14	0.76
	Recruitment	Beta (1,1)	0.16	0.08	0.29
	N_{Super}		159	131	174
	N_{Mean}		61	35	108
γ(Survey)	Recapture (Survey)	Beta (1,1)	0.16	0.09	0.25
	Recapture (Other)	Beta (1,1)	0.02	0.01	0.05
	Apparent survival	Beta (1,1)	0.26	0.11	0.49
	Recruitment (Survey)	Beta (1,1)	0.03	0.01	0.07
	Recruitment (Other)	Beta (1,1)	0.58	0.38	0.82
	N_{Super}		169	156	174
	N_{Mean}		45	31	69

Figure 6. Sampling trip-specific abundance estimates and 95% credible intervals (CRI) *Thamnophis elegans* (THEL) at Canyon Creek, Arizona during 2022–2024 for models assuming constant recruitment probability (Gamma(.)) and recruitment probability varying between Survey and Other sampling trips (Gamma(Survey)). Solid and dashed dark gray lines represent the mean and 95% CRI, respectively, abundance estimate across all sampling trips for the Gamma(.) model and the solid and dashed light gray lines represent the mean and 95% CRI, respectively, abundance estimates across all sampling trips for the Gamma(Survey) model.

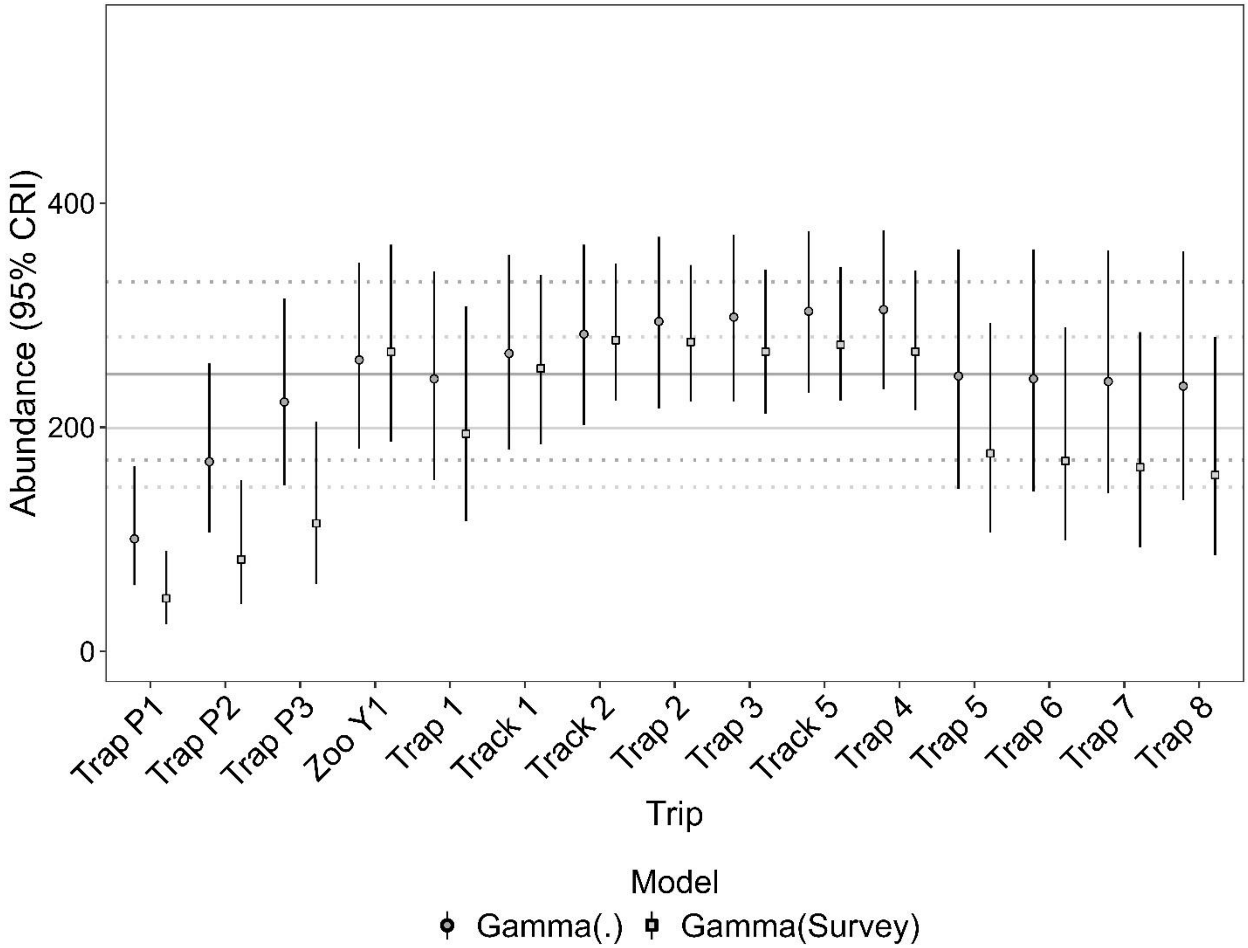


Table 8. Model parameters, prior distributions, and posterior means (Mean) and quantile-based 95% credible interval (CRI) from a Jolly-Seber survival model fit using mark-recapture data from *Thamnophis elegans* (THEL) at Canyon Creek, Arizona, during 2022–2024. Model parameters include recapture probability (p), annual apparent survival (φ), and recruitment probability (γ). Abundance (N) is estimated as a derived parameter. Surveys are sessions using both VES and trapping and Other are sessions including tracking or release sessions. Super population size (N_{Super}) represents the estimated total number of individuals entering the study population during the study period. Mean abundance (N_{Mean}) is the average abundance estimate across all sampling occasions. Results are presented for models assuming constant γ (γ(.)) and allowing γ to vary between Surveys and Other (γ(Survey)).

Model	**Parameter**	**Prior**	**Mean**	**LCRI**	**UCRI**
γ(.)	Recapture (Survey)	Beta (1,1)	0.05	0.04	0.08
	Recapture (Other)	Beta (1,1)	0.02	0.01	0.03
	Apparent survival	Beta (1,1)	0.73	0.50	0.94
	Recruitment	Beta (1,1)	0.25	0.15	0.40
	N_{Super}		396	372	405
	N_{Mean}		248	171	330
γ(Survey)	Recapture (Survey)	Beta (1,1)	0.07	0.05	0.10
	Recapture (Other)	Beta (1,1)	0.02	0.01	0.03
	Apparent survival	Beta (1,1)	0.58	0.38	0.83
	Recruitment (Survey)	Beta (1,1)	0.11	0.05	0.22
	Recruitment (Other)	Beta (1,1)	0.56	0.31	0.86
	N_{Super}		398	376	405
	N_{Mean}		199	146	281

Discussion

Our results indicate broadly similar patterns of individual growth, movement, and apparent survival between syntopic THRU and THEL at Canyon Creek. Although these species differ in their imperilment status and multiple aspects of their ecology, the demographic and behavioral similarities we observed suggest that both species currently exhibit robust populations in Canyon Creek. We regularly captured neonates of both THEL and THRU during each year of our study which likely indicates healthy reproductive populations. However, additional long-term demographic data and information on other demographic parameters (e.g., fecundity, abundance) are needed to fully evaluate these populations. Our estimates of abundance for these two species suggest that THEL are more numerous than THRU at our study site and we did capture over twice as many THEL as THRU. The highly similar recapture probabilities for these species during Survey sessions suggest that greater captures of THEL is indeed due to greater abundance of this species and not because THEL is necessarily more conspicuous or easier to capture. We captured substantially fewer THCY than either THRU or THEL, which may be due in part to the elevation of the study site being near the upper elevational limit for THCY. Nevertheless, we did observe multiple neonate and adult THCY at Canyon Creek which indicates a reproducing population. It is possible that ecological differences between syntopic THEL and THRU could be exacerbated in environments that were less suitable for THRU although comparative studies at other locations are needed to fully test this hypothesis.

Although recapture probabilities during VES and trapping surveys were similar for both species, our CPUE results provide some insights on the efficacy of different sampling methods for gartersnakes in southwestern stream environments. VES appeared to be the most effective method overall for capturing both THRU and THEL compared to trapping. The success of formal VES is noteworthy as it has not been consistently applied or compared to trapping at all *Thamnophis* study sites. However, Ryan et al. (2019) did find that previous gartersnake surveys at Canyon Creek generally captured more THRU and THEL during VES compared to trapping. CPUE from VES in our study was significantly higher for THEL than for THRU. The difference in VES-based CPUE and our survey-based recapture probabilities could be due to combining VES and trapping within our CJS model. Differences in VES-based CPUE could reflect differences in species behavior and movement within the riparian environment whereas THRU seemed to be more secretive and less likely to be found out in the open.

Estimated annual apparent survival probabilities for both THRU and THEL were generally lower than those reported from other mark-recapture *Thamnophis* studies. Bronikowski and Arnold (1999) reported wide variation in apparent annual survival of adult THEL among five study sites in the Cascade Mountains of central Oregon. They reported 95% CI for adult annual apparent survival of 0.34–0.40 and 0.55–0.57 among two lake populations and 0.71–0.76, 0.74–0.78, and 0.76–0.86 among three meadow populations. They also reported markedly lower annual apparent survival rates for juvenile THEL (95% CI = 0.14–0.21 and 0.19–0.19 for the two lake populations and 0.27–0.50, 0.23–0.33, and 0.22–0.44 for the three meadow populations). Lind et al. (2005) reported annual apparent survival estimates for *T. atratus hydrophilus* in northwestern California of 0.56 (± 0.03 SE) for males and 0.65 (± 0.02 SE) for females. Rose et al. (2018b) estimated annual apparent survival for *T. gigas* across 10 sites in the Central Valley of California and lowest and highest site-specific annual apparent survival estimates were 0.35 (0.17–0.56) and 0.59 (0.47–0.73), respectively. The lack of consistency in how survival estimates are reported in these studies limits our ability to make direct comparisons among studies. A potential limitation of estimating survival using the CJS model is that it cannot distinguish between survival and permanent emigration. This may have contributed to the annual apparent survival estimates for THRU and THEL in our study being lower than values reported for other *Thamnophis* species. We were unable to evaluate the extent of permanent emigration within our study system although the scale of observed gartersnake movements relative to the scale of our survey reach do indicate that it is possible for gartersnakes we captured to move outside of the survey reach. Our relatively short study duration combined with relatively low recapture rates may have also influenced our survival estimates. Low recapture rates are common in mark-recapture studies across snake taxa (Lind et al. 2005; Durso et al. 2011; Rose et al. 2018b) but these generally act to reduce the precision of parameter estimates in survival models instead of biasing those estimates low. We conducted some preliminary simulation analyses of our CJS analyses using the number of sampling events and marked individuals observed in our study and found that even when apparent survival is <0.50 our models still returned unbiased estimates of apparent survival (unpublished data). Additional years of mark-recapture surveys at Canyon Creek could provide additional data to further refine these survival estimates.

Our study provides model-based estimates of abundance for THRU that were reasonably precise and suggested an average abundance within our 1.7 km survey reach of approximately 45-61 individuals. This corresponds to a linear density of individuals of 26-36 individuals per kilometer. Model-based abundance estimates for gartersnakes are relatively scarce although Lind et al. (2005) reported a linear density of 58-131 individuals per kilometer of stream for *T. atratus hydrophilus* in northwestern California. We marked a total of 61 THRU during our entire study which may suggest that our abundance estimates for THRU were low. Estimating abundance for snake populations is generally difficult due to their cryptic nature and typically low capture/recapture rates (Steen 2010; Durso et al. 2011). These factors also make it challenging to collect sufficient data that also conform to the assumptions of mark-recapture models for abundance estimation. Our sampling design of multiple multi-day survey and trapping sessions separated by a few weeks to an entire winter is amenable to a robust design model which permits the estimation of both apparent survival and abundance (Pollock et al. 1990; Willson et al. 2011). However, when considering only the data used to fit our JS model, we only recaptured five individual THRU at least twice within the same sampling session and these within-session recaptures only occurred on three of 13 sampling sessions (Trap 3, Trap 4, and Trap 6; Table 1). These data were likely too sparse to reliably estimate the parameters from a robust design model. Although the JS model can be used to estimate abundance from an open population (i.e., a population subject to births, deaths, immigration, and emigration during the study period), the JS model assumes that the probability of capturing an unmarked individual and the probability of recapturing a marked individual are the same. Although the validity of this assumption is largely unknown for snakes, there is some evidence that snakes may alter their behavior to become less conspicuous after marking (Brown 2008). Such a "capture-shy' response does not affect recapture and apparent survival estimates from a CJS model because the CJS model only incorporates data post-capture to estimate model parameters. Additional sources of unmodeled heterogeneity in capture rates could come from unmodeled temporal variation in sampling effort (e.g., shorter survey sessions during 2022 [Table 1]) or snake activity (e.g., early summer vs. late summer). Because of the reliance of JS model abundance estimates on these assumptions, we advise caution when making inferences based on these abundance estimates.

Our VHF telemetry data indicated that telemetered snakes were often away from water and outside of areas we would normally survey during VES. This finding could point to snakes accessing the water less than expected, and indicate a potential factor contributing to our low recapture rates. However, the short telemetry tracking durations limit our ability to make inferences about gartersnake movements in Canyon Creek. Although other gartersnake studies have had success with external transmitter placement described by Wylie et al. (2011) on *T. gigas*, including a study on *T. eques* (Sprague and Bateman 2018) and THCY (Blais et al. 2023), we had difficulty maintaining transmitter attachment. We found that the duration of transmitter attachment was influenced by the snake's behavior and how quickly the snake would access the water. For example, the transmitters that remained attached the longest, and our only instance keeping the transmitter attached until ecdysis, came from large gravid THEL females that remained in terrestrial shelter sites for relatively long periods and did not cross Canyon Creek during this time. In contrast, we observed multiple instances where a transmitter apparently became unattached shortly after a snake crossed Canyon Creek. We also had adverse effects of different types of tapes on the snakes that led us to remove transmitters from THRU and only continue telemetry with THEL and THCY. We never exceeded the width of the body with transmitters or 5% of body mass, but for future external attachments of VHF transmitters we suggest prioritizing using the smallest possible transmitters that will work within the design of the study.

The application of the passive PIT tag arrays for monitoring aquatic snakes showed potential as a useful method to help increase recapture rates. These arrays provided recaptures on several individuals that were not recaptured or were recaptured less frequently through VES and trapping and documented multi-season survival for individuals of both species that were not physically captured during 2024. The passive PIT tag arrays also documented that both species remained surface-active along Canyon Creek into early October 2024. However, passive PIT tag arrays only increased recapture probability for THRU and not for THEL. This likely reflects our placement of our four passive PIT tag arrays which were intentionally placed in areas with relatively high numbers of THRU captures during 2022–2023. We did this to maximize the chances of detecting THRU because of uncertainties about how this technology would perform in this novel application. This information is nevertheless valuable because THRU appear to be more difficult than THEL to find within Canyon Creek.

In conclusion, this study indicates similarities in multiple ecological and demographic traits between sympatric gartersnakes at Canyon Creek, including the federally threatened THRU. This comparison is valuable because it could indicate that there is not some inherent difference between these species that would cause different species-specific population declines in the same system that is able to support their needs. The use of VES for monitoring these species was effective, along with implementation of the passive PIT units to help gain more accurate information about survival and recapture rates. Applying all of these methods (VES, trapping, passive PIT tag arrays) consistently for future work may yield increasingly reliable comparison between methods along with additional seasons of monitoring to evaluate survival estimates. Gathering these data from other sites where both species occur that can be compared directly would also be very important to increase our understanding of these species' population ecology.

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