

POPULATION ECOLOGY AND CONSERVATION TRANSLOCATION OF THE
NARROW-HEADED GARTERSNAKE IN CENTRAL ARIZONA

by

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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 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 the management and conservation of this species. We conducted a three-year mark-recapture study of narrow-headed gartersnakes in Canyon Creek in central Arizona. In chapter 1, we compared capture rates, individual growth rates, movement, and apparent survival between narrow-headed gartersnakes and a syntopic, non-imperiled species of gartersnake, the western terrestrial gartersnake (*Thamnophis elegans*). While we captured more western terrestrial gartersnakes during our study, we did not find marked differences between these two species in the metrics we examined. We also documented the successful application of passive PIT tag arrays for monitoring PIT-tagged gartersnakes. In chapter 2, we evaluated the post-release growth, movement, and apparent survival zoo-born narrow-headed gartersnakes from the Arizona Center for Nature Conservation/Phoenix Zoo's breeding program and compared these metrics to those of wild narrow-headed gartersnakes. We released four different groups of zoo-born individuals representing two cohorts (young-of-year and holdover). We documented multiple instances of survival across one and two winters post-release by zoo-born individuals from The Arizona Center for Nature Conservation/Phoenix Zoo. We did not find marked differences between zoo-born and wild individuals although holdover individuals tended to have the greatest movement distances and lowest apparent survival. Our results can provide guidelines for the future use of conservation translocations for narrow-headed gartersnake recovery.

Chapter 1: Comparative Demography, Movements, and Growth of Three Syntopic Gartersnakes in Central Arizona

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 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 also 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 population 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 (Flehart 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 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 across much of western North America and is not of conservation concern (Stebbins 2003, Hallas et al. 2021). In Arizona, THEL inhabits a broad elevation range and from Great Basin Desertscrub to Rocky Mountain Montane Conifer forest and , while also associated with riparian and wetland environments, will use a much greater 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 at 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 biology 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 within the southwestern USA and compare these traits among these species. Our specific objectives were to estimate and compare: 1) encounters (i.e., catch per unit effort) using visual encounter surveys and passive trapping, 2) movement patterns, 3) individual growth rates, and 4) apparent survival and recapture probabilities.

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 (Fig. 1.1). 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*).

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 mudsnails (*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 (2–8 night, mean ~5 days) survey/trapping sessions (hereafter survey sessions) 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 of our survey reach. We also recorded the 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 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.

We placed 35–111 Gee® minnow traps with 3.175mm 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 ~15m 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 1.1 & 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 1.1 & 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 the CPUE calculations.

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 (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 PIT tags (12.5 mm l x 2.03 mm d, 134.2 kHz) in 2023–2024) and nine snakes with Biomark HDX12 PIT tags (12 mm l x 2.12 mm, 134.2 kHz) in 2022. Both types of PIT tags applied are readable by universal PIT tag scanners. We collected blood samples from each captured snakes 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. This method 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, 132.4kHz) 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 the presence of 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 second 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 1.3).

Radio Telemetry

We attached VHF temperature-sensitive radio transmitters (PD-2T 2.5g and BD-2T 1.8 g, Holohil, Carp, Ontario, Canada) externally to select gartersnakes. Transmitters were $\leq 5\%$ of the snake’s body weight and did not exceed the gartersnake’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. $\frac{3}{4}$ 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 their 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 survey session of 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). When time permitted, we located telemetered snakes up to three times per day. 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 or not the snake was visible or seen with the transmitter still attached, and any observed behavior.

Analysis

Since 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 within 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), that 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 was nonnormally distributed. We used t-tests to compare CPUE between trapping and 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 identify 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 (L_{inf}), 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 (λ). 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 (L_{inf} , k , and λ) 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 1.4) as necessary to ensure sufficient model convergence (c.f., Rose et al. 2018a, 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 which could potentially increase 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 interactive function 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 [see Chapter 2]). 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).

Results

Surveys Summary

During our 15 different survey sessions we captured and marked 61 THRU with a total of 81 captures (Table 1.1), marked 131 THEL with a total of 161 captures (Table 1.2), and marked 8 THCY with a total of 9 (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. The peak in captures for THRU occurred during August in each year reflected the presence of

neonates although the greatest number of captures occurred during either June or July sessions for THEL (Tables 1.1 & 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 our 11 sampling periods between mid-May and early October (Table 1.3). 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 (Fig. 1.2). There was no evidence that passive PIT tag array CPUE 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; $t = 0.745_{19,996}$, $P = 0.465$). 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; $t = 1.394_{11,061}$, $P = 0.191$). 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; $t = 2.304_{13,345}$, $P = 0.038$).

Growth Rate

We obtained 18 change (Δ) in SVL measurements 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). While THRU had greater changes in SVL between consecutive recaptures (mean = $\Delta 77.60$ mm, SD = 86.13) than THEL (mean = $\Delta 25.92$ 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 = $\Delta 20.73$ mm, $SD = 28.62$) than females (mean = $\Delta 71.00$ 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 change (Δ) in weight measurements from 17 gartersnakes (10 THEL and seven 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 = $\Delta 9.29$ g, $SD = 12.56$) and THEL (mean = $\Delta 8.42$ 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 = $\Delta 6.36$, $SD = 7.70$; Females: mean = $\Delta 12.00$, $SD = 16.35$; $\beta_{\text{Male}} = -5.27$, $P = 0.275$). 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 captured at larger weights had less change in weight between consecutive recaptures ($\beta_{\text{First_Weight}} = -0.22$, $P = 0.044$).

We used SVL measurements from 191 individuals (57 THRU and 134 THEL) to fit our von Bertalanffy growth model. We had eight individual THRU with more than one SVL measurement and 12 individual THEL with more than one SVL. Number of days between recaptures ranged from 23 to 378 days (median = 287 days). Our von Bertalanffy 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 1.4). The strongest effect was for higher individual heterogeneity in growth rate for males ($\lambda_{\text{MALE}} = 164.98$, 95% CRI = 139.50–650.40, PP = 0.78).

Movement

We attached external VHF transmitters to six THRU, 10 THEL and one THCY and found that transmitters generally came off the snakes in less than two weeks, although in six cases (one THRU, five THEL) within 24 hrs after attachment (Table 1.5). 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 duration ranged from 2–42 days (mean = 18.4 days SD = 6.7; $N = 1$ male, 4 females), and THCY duration was four days (1 female). Due to the 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 five for THCY and from these we found that all three species remained relatively close to the stream. The furthest distance THRU moved from the stream was 34 m by a female on 8 June 2023, whereas one female THEL and THCY moved slightly further, 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 glue or other issues. Out of an abundance of caution for the snake's wellbeing we removed all the transmitters and ceased further telemetry.

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) while 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 not show any evidence of a difference ($\beta_{\text{THRU}} = 0.04$, $P = 0.926$). These results indicated that THRU made generally shorter movements downstream while THEL made markedly longer movements downstream (Fig. 1.3). 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. 1.4).

Survival

We used mark-recapture data from 58 THRU (27 males and 31 females) and 135 THEL (76 males, 57 females, and two of unknown sex). Amongst individuals recaptured on 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, relatively so, between THRU and THEL ($p < 0.07$,

Table 1.6), 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 1.6). 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 ($\beta = 0.18$, 95% CRI -0.43–0.82, PP = 0.73). Annual apparent survival estimates for an average-size individual were similar between species (THRU: $\phi = 0.30$, 95% CRI = 0.15–0.52; THEL: $\phi = 0.35$, 95% CRI = 0.16–0.62; Table 1.6).

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 observed in our study suggests 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. Although we were not able to formally estimate abundance, we captured over twice as many THEL as THRU. The highly similar recapture probabilities for these species during Survey sessions suggests that the greater captures of THEL is due to a 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.

Our 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 adult THEL annual apparent survival 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 in this populations (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 captured anywhere in our survey reach to move outside of the survey reach. The relatively short duration of our study may have also resulted in a confounding of temporary and permanent emigration. 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 our results indicate 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 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 with 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 become 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 traits between sympatric gartersnakes, including the federally threatened THRU, at Canyon Creek. This comparison is valuable because it could indicate that there is not some inherent difference between these species that would cause a decline in the same system that is able to support their needs. The use of VES for monitoring these species was indicated to be effective, along with implementation of the passive PIT units to help gain more accurate information about survival and recapture rates. We recommend that all these methods (VES, trapping, passive PIT tag arrays) be applied consistently for future work for the most accurate comparison between methods along with additional seasons of monitoring to evaluate survival estimates. Gaining this data from other sites where both species occur and analysis that can be directly compared would also be very important to the understanding of these species' population ecology.

Figure 1.1. 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.

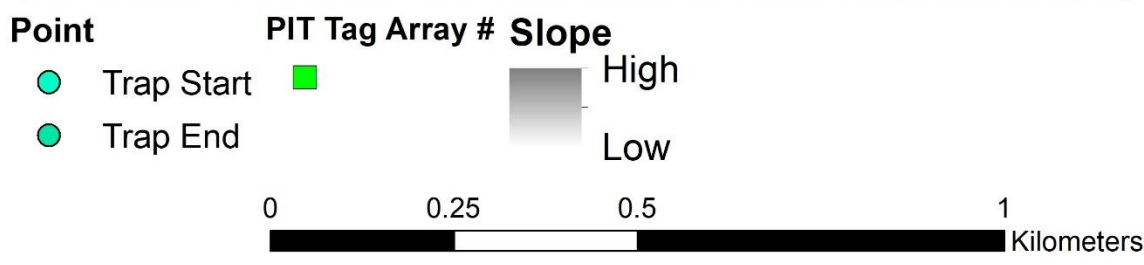
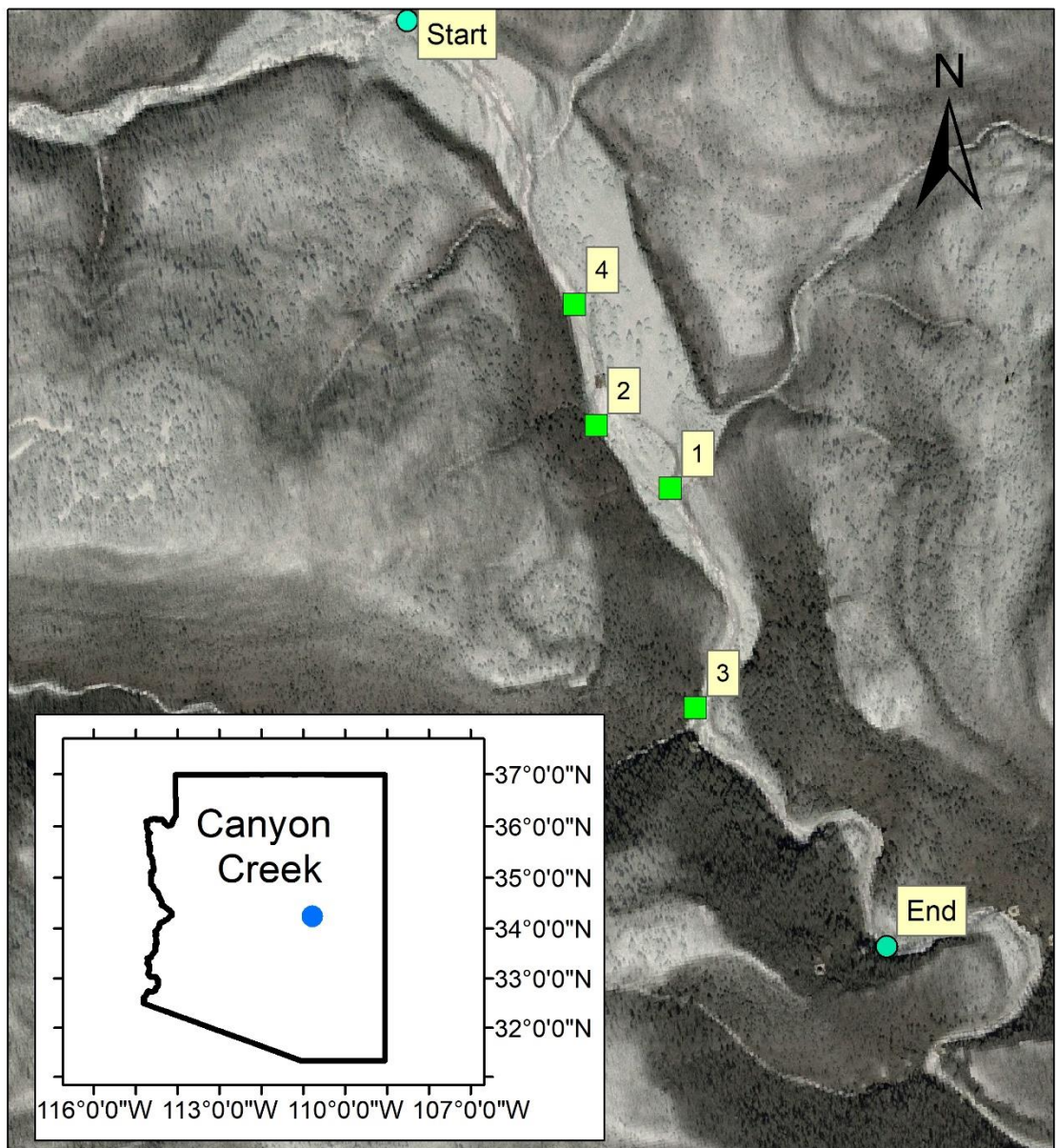


Table 1.1. Survey and trapping effort and success for *Thamnophis rufipunctatus* (THRU) using visual encounter survey (VES) and aquatic minnow traps at Canyon Creek, Arizona, during 2022–2024. Trip types are: Trap (VES and trapping), Track (sessions focused on radio telemetry monitoring), and Zoo (release 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	22.63	0	0	1	1	0.000	0.000
2022	Trap P2 July (11-13)	107	214	5136	8.80	0	0	0	0	0.000	0.000
2022	Trap P3 July (18-21)*	35	85	2040	22.25	1	1	0	2	4.494	0.049
2022	Zoo Y1 August 15	0	NA	NA	22.50	3	0	0	3	13.333	NA
2022	TOTALS	223	459	11016	76.18	4	1	1	6	5.251	0.009
2023	Trap 1 May (24-30)*	85	506	12144	67.62	5	5	1	11	7.394	0.041
2023	Track 1 June (6-9)*	50	147	3528	27.90	1	1	1	3	3.584	0.028
2023	Track 2 June (12-15)	0	NA	NA	37.65	3	0	0	3	7.968	NA
2023	Trap 2 June (21-28)*	100	694	16656	84.10	3	9	1	13	3.567	0.054
2023	Trap 3 July (19-26)*	102	687	16488	72.90	1	3	2	6	1.372	0.018
2023	Track 5 August (1-3)	0	NA	NA	6.03	0	0	0	0	0.000	NA
2023	Trap 4 August (16-23)*	108	747	17928	91.60	9	10	4	23	9.825	0.056
2023	TOTALS	445	2781	66744	387.80	22	28	9	59	5.673	0.042
2024	Trap 5 May (22-26)	111	479.5	11508	63.33	1	0	0	1	1.579	0.000
2024	Trap 6 June (19-26)*	105	735	17640	73.52	2	4	0	6	2.720	0.023
2024	Trap 7 July (17-20)*	110	385	9240	54.72	0	2	0	2	0.000	0.022
2024	Trap 8 August (19-20)*	40	60	1440	17.37	0	4	3	7	0.000	0.278
	TOTALS	366	1659.5	39828	208.94	3	10	3	16	1.436	0.025
2022-2024	Combined TOTALS	1034	4899.5	117588	672.93	29	39	13	81	4.310	0.033

Table 1.2. 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	22.63	6	2	0	8	26.513	0.052
2022	Trap P2 July (11-13)	107	214	5136	8.80	3	0	0	3	34.091	0.000
2022	Trap P3 July (18-21)*	35	85	2040	22.25	1	3	0	4	4.494	0.147
2022	TOTALS	223	459	11016	53.68	10	5	0	15	18.629	0.045
2023	Trap 1 May (24-30)*	85	506	12144	67.62	10	3	2	15	14.789	0.025
2023	Track 1 June (6-9)*	50	147	3528	27.90	8	1	0	9	28.674	0.028
2023	Track 2 June (12-15)	0	NA	NA	37.65	9	0	0	9	23.904	NA
2023	Trap 2 June (21-28)*	100	694	16656	84.10	2	10	7	19	2.378	0.060
2023	Trap 3 July (19-26)*	102	687	16488	72.90	8	14	4	26	10.974	0.085
2023	Track 5 August (1-3)	0	NA	NA	6.03	1	0	0	1	16.576	NA
2023	Trap 4 August (16-23)*	108	747	17928	91.60	5	5	10	20	5.459	0.028
2023	TOTALS	445	2781	66744	387.80	43	33	23	99	11.088	0.049
2024	Trap 5 May (22-26)	111	479.5	11508	63.33	8	4	1	13	12.632	0.035
2024	Trap 6 June (19-26)*	105	735	17640	73.52	5	8	1	14	6.801	0.045
2024	Trap 7 July (17-20)*	110	385	9240	54.72	3	8	1	12	5.482	0.087
2024	Trap 8 August (19-20)*	40	60	1440	17.37	8	0	0	8	46.056	0.000
	TOTALS	366	1659.5	39828	208.94	24	20	3	47	11.486	0.050
2022-2024	Combined TOTALS	1034	4899.5	117588	650.43	77	58	26	161	11.838	0.049

Table 1.3. 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 column represents 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

Figure 1.2. Detections of *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) by four passive PIT (passive integrated transponder) 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).

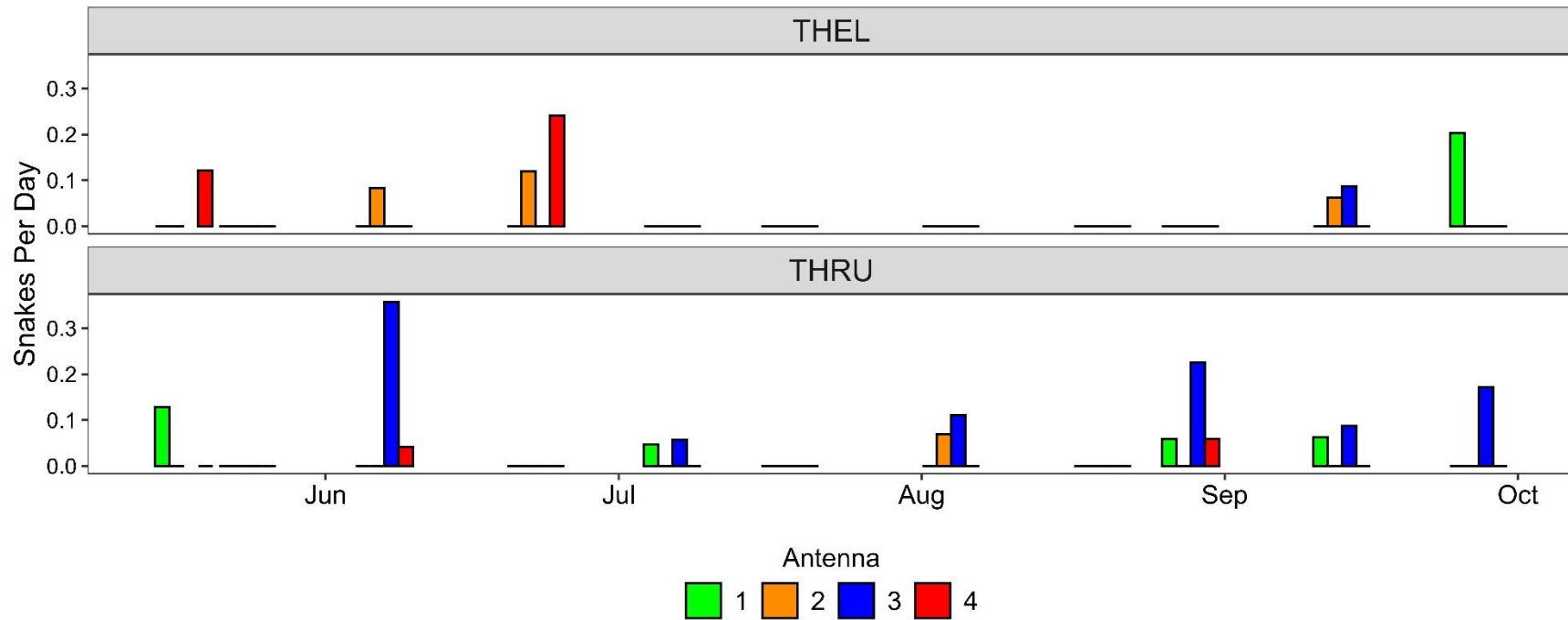


Table 1.4. Model parameters, prior distributions, and posterior means (Mean), quantile-based 95% credible interval (CRI), and posterior probabilities (PP) from a Von Bertalanffy growth model fit to snout vent length data from *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) at Canyon Creek, 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

Table 1.5. 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 pulled 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 (m)	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

Table 1.6. 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. $\beta(\text{SVL})$ is the slope estimate for an additive effect of SVL as a time-varying individual covariate on for both p and ϕ predicted from our 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
Recapture	THRU Surveys	Beta (1,1)	0.065	0.028	0.12	1
Recapture	THEL Antenna	Beta (1,1)	0.027	0.010	0.053	1
Recapture	THRU Antenna	Beta (1,1)	0.211	0.106	0.339	1
Recapture	Other Session	Beta (1,1)	0.026	0.009	0.053	1
Recapture	$\beta(\text{SVL})$	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
Survival	THRU ϕ	Beta (1,1)	0.304	0.147	0.516	1
Survival	$\beta(\text{SVL})$	Normal (0,1.648)	0.183	-0.433	0.815	0.726

Figure 1.3. 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.

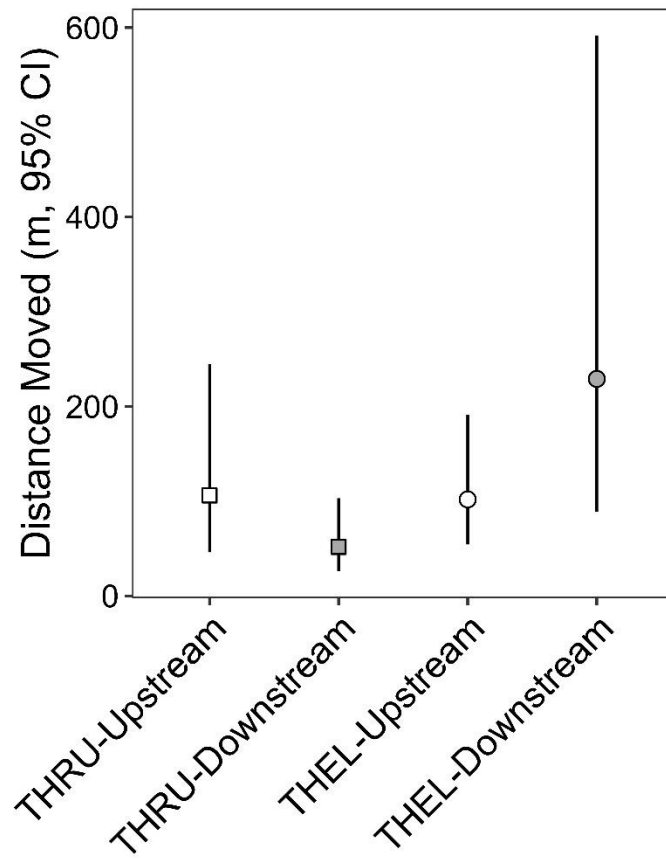
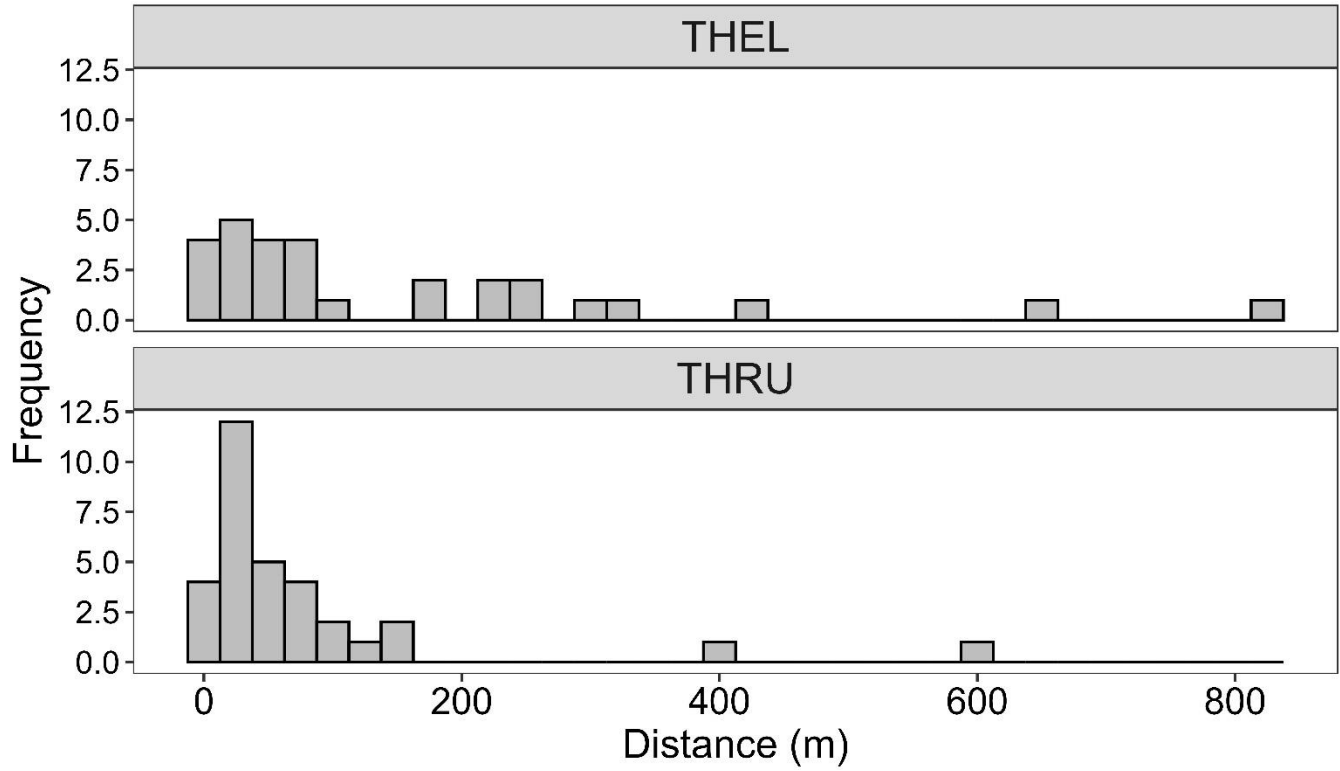


Figure 1.4. Histogram of Euclidean distances (m) between consecutive recaptures for *Thamnophis rufipunctatus* (THRU) and *T. elegans* (THEL) at Canyon Creek, Arizona during 2022–2024.



Literature Cited

- Andrews, R. M. 1979. The Lizard *Corytophanes cristatus*: An Extreme “Sit-and-Wait” Predator. *Biotropica* 11:136.
- Blais, B. R., S. L. Johnson, and J. L. Koprowski. 2023. Effects of disturbances and environmental changes on an aridland riparian generalist. *PeerJ* 11:e15563.
- Bronikowski, A. M. 2000. Experimental Evidence for the Adaptive Evolution of Growth Rate in the Garter Snake *Thamnophis elegans*. *Evolution* 54:1760–1767.
- Bronikowski, A.M., and S.J. Arnold. 1999. The Evolutionary Ecology of Life History Variation in The Garter Snake *Thamnophis Elegans*. *Ecology* 80:2314–2325. DOI: [https://doi.org/10.1890/0012-9658\(1999\)080\[2314:TEEOLH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2314:TEEOLH]2.0.CO;2)
- Brooks, M., E., K. Kristensen, K. Benthem J. ,van, A. Magnusson, C. Berg W., A. Nielsen, H. Skaug J., M. Mächler, and B. Bolker M. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9:378.
- Brooks, S. P., and A. Gelman. 1998. General Methods for Monitoring Convergence of Iterative Simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- Brown, D. E., and C. H. Lowe. 1995. Biotic Communities: Southwestern United States and Northwestern Mexico. *Taxon* 44:659.
- Brown, W. S. 2016. Lifetime Reproduction in a Northern Metapopulation of Timber Rattlesnakes (*Crotalus horridus*). *Herpetologica* 72:331–342.
- Caughley, G. 1994. Directions in Conservation Biology. *Journal of Animal Ecology* 63:215–244.
- Chandler, H. C., D. Steen, J. Blue, J. E. Bogan, M. R. Bolt, T. Brady, D. R. Breininger, J. Buening, M. Elliott, J. Godwin, C. Guyer, R. L. Hill, M. Hoffman, N. L. Hyslop, C. L. Jenkins, C. Lechowicz, M. Moore, R. A. Moulis, S. Piccolomini, R. Redmond, F. H. Snow, B. S. Stegenga, D. J. Stevenson, J. Stiles, S. Stiles, M. Wallace, J. Waters, M. Wines, and J. M. Bauder. 2023. Evaluating Growth Rates of Captive, Wild, and Reintroduced Populations of the Imperiled Eastern Indigo Snake (*Drymarchon couperi*). *Herpetologica* 79.
- Cole, K. 2023. Canyon Creek Fish Survey Report. July 23, 2023. Arizona Game and Fish Department. 13 pp.

- Cormack, R. M. 1964. Estimates of Survival from the Sighting of Marked Animals. *Biometrika* 51:429–438.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* 14:405–410.
- Drost, C. A. 2020. *Thamnophis elegans* Terrestrial Gartersnake. Pages 401–417 in A. Holycross and J. Mitchell, editors. *Snakes of Arizona*. E. C. O. Herpetological Publishing & Distribution.
- Durso, A. M., J. D. Willson, and C. T. Winne. 2011. Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation* 144:1508–1515.
- Durso, A. M., J. D. Willson, and C. T. Winne. 2013. Habitat influences diet overlap in aquatic snake assemblages. *Journal of Zoology* 291:185–193.
- Eaton, M. J., and W. A. Link. 2011. Estimating age from recapture data: integrating incremental growth measures with ancillary data to infer age-at-length. *Ecological Applications* 21:2487–2497.
- Engelstoft, C., and K. E. Ovaska. 2000. Artificial Cover-Objects as a Method for Sampling Snakes (*Contia tenuis* and *Thamnophis* spp.) in British Columbia. *Northwestern Naturalist* 81:35.
- Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265–289.
- Fleharty, E. D. 1967. Comparative Ecology of *Thamnophis elegans*, *T. cyrtopsis*, and *T. rufipunctatus* in New Mexico. *The Southwestern Naturalist* 12:207.
- Gaind, N. 2016. Wildlife in decline: Earth's vertebrates fall 58% in past four decades. *Nature*. <https://doi.org/10.1038/nature.2016.20898>.
- Gaston, K. J., and T. M. Blackburn. 1995. Rarity and Body Size: Some Cautionary Remarks. *Conservation Biology* 9:210–213.

- Gelman, A., and J. Hill. 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York.
- Gerritsen, J., and J. R. Strickler. 1977. Encounter Probabilities and Community Structure in Zooplankton: a Mathematical Model. *Journal of the Fisheries Research Board of Canada* 34:73–82.
- Gomez, L., K. W. Larsen, and Patrick. T. Gregory. 2015. Contrasting Patterns of Migration and Habitat Use in Neighboring Rattlesnake Populations. *Journal of Herpetology* 49:371–376.
- Hallas, J. M., T. L. Parchman, and C. R. Feldman. 2021. The influence of history, geography and environment on patterns of diversification in the western terrestrial garter snake. *Journal of Biogeography* 48:2226–2245.
- Halstead, B. J., G. D. Wylie, and M. L. Casazza. 2013. Efficacy of Trap Modifications for Increasing Capture Rates of Aquatic Snakes in Floating Aquatic Funnel Traps. *Herpetological Conservation and Biology* 8:65–74.
- Hebard, W. B. 1951. Notes on the Ecology of Gartersnakes in the Puget Sound Region. *Herpetologica* 7:61–62.
- Hernández-Yáñez, H., S. Y. Kim, and J. P. Che-Castaldo. 2022. Demographic and life history traits explain patterns in species vulnerability to extinction. M. Fujiwara, editor. *PLOS ONE* 17:e0263504.
- Holliday, R. 2005. Ageing and the extinction of large animals. *Biogerontology* 6:151–156.
- Holycross, A., J. Mitchell, A. T. Holycross, E. M. Nowak, B. L. Christman, and R. D. Jennings. 2020. *Thamnophis rufipunctatus* Mogollon Narrow-Headed Gartersnake. Pages 440–455 *in*. *Snakes of Arizona*. E. C. O. Herpetological Publishing & Distribution.
- Holycross, A. T., T. C. Brennan, and R. D. Babb. 2022. A field guide to Amphibians and Reptiles in Arizona. Second. Arizona Game and Fish Department.
- Huey, R. B., and E. R. Pianka. 1981. Ecological Consequences of Foraging Mode. *Ecology* 62:991–999.

- Jenkins, C. L., C. R. Peterson, S. C. Doering, and V. A. Cobb. 2009. Microgeographic Variation in Reproductive Characteristics among Western Rattlesnake (*Crotalus oreganus*) Populations. *Copeia* 2009:774–780.
- Jolly, G. M. 1965. Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. *Biometrika* 52:225–247.
- Jones, T. R., and F. R. Hensley. 2020. *Thamnophis cyrtopsis* Black-necked Gartersnake. Pages 388–400 in A. Holycross and J. Mitchell, editors. *Snakes of Arizona*. E. C. O. Herpetological Publishing & Distribution.
- Kellner, K. 2015. jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses. CRAN: Contributed Packages. <https://doi.org/10.32614/cran.package.jagsui>.
- Kephart, D. G. 1982. Microgeographic variation in the diets of garter snakes. *Oecologia* 52:287–291.
- Kephart, D. G., and S. J. Arnold. 1982. Garter Snake Diets in a Fluctuating Environment: A Seven-Year Study. *Ecology* 63:1232–1236.
- Lind, A. J., H. H. Welsh, and D. A. T. R. work(s): 2005. Garter Snake Population Dynamics from a 16-Year Study: Considerations for Ecological Monitoring. *Ecological Applications* 15:294–303.
- Major, T., D. R. Atkins, L. Jeffrey, and W. Wüster. 2020. Marking the un-markable: visible implant elastomer in wild juvenile snakes. *Herpetological Journal* 173–176.
- Manier, M. K., and S. J. Arnold. 2005. Population genetic analysis identifies source–sink dynamics for two sympatric garter snake species (*Thamnophis elegans* and *Thamnophis sirtalis*). *Molecular Ecology* 14:3965–3976.
- Mawdsley, J. R., R. O’Malley, and D. S. Ojima. 2009. A Review of Climate-Change Adaptation Strategies for Wildlife Management and Biodiversity Conservation. *Conservation Biology* 23:1080–1089.
- Oldham, C. R., J. L. Fleckenstein III, W. A. Boys, and S. J. Price. 2016. Enhancing Ecological Investigations of Snakes with Passive Integrated Transponder (PIT) Tag Telemetry. *Herpetological Review* 47:385–388.

- Parker, W. S., and M. V. Plummer. 1987. Population ecology. Pages 253–301 in R. A. Seigel, J. T. Collins, and S. S. Novak, editors. *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Company, New York.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003).
- R Core Team. 2024. R: A language and environment for statistical computing. <<<https://www.R-project.org/>>>.
- Reinhardt, K., G. Köhler, S. Maas, and P. Detzel. 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. *Ecography* 28:593–602.
- Robinson, J. G. 2006. Conservation Biology and Real-World Conservation. *Conservation Biology* 20:658–669.
- Roe, J. H., B. A. Kingsbury, and N. R. Herbert. 2004. Comparative water snake ecology: conservation of mobile animals that use temporally dynamic resources. *Biological Conservation* 118:79–89.
- Rose, J. P., B. J. Halstead, G. D. Wylie, and M. L. Casazza. 2018a. Spatial and Temporal Variability in Growth of Giant Gartersnakes: Plasticity, Precipitation, and Prey. *Journal of Herpetology* 52:40–49.
- Rose, J. P., G. D. Wylie, M. L. Casazza, and B. J. Halstead. 2018b. Integrating growth and capture–mark–recapture models reveals size-dependent survival in an elusive species. *Ecosphere* 9:e02384.
- Ryan, M. J., A. B. Smith, S. Lashway, K. K. Smith, S. B. Riddle, C. M. Akins, B. R. Blais, and K. T. Krahn. 2019. A five-year narrow-headed gartersnake (*Thamnophis rufipunctatus*) survey summary from Canyon Creek, Arizona. Nongame and Endangered Wildlife Program Technical Report 323. Arizona Game and Fish Department, Phoenix, Arizona.
- Salt, G. W. 1967. Predation in an Experimental Protozoan Population (*Woodruffia-Paramecium*). *Ecological Monographs* 37:113–144.
- Schoener, T. W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics* 2:369–404.

- Seber, G. A. F. 1965. A Note on the Multiple-Recapture Census. *Biometrika* 52:249–259.
- Sprague, T. A., and H. L. Bateman. 2018. Influence of seasonality and gestation on habitat selection by northern Mexican gartersnakes (*Thamnophis eques megalops*). C. M. Somers, editor. *PLOS ONE* 13:e0191829.
- Stebbins, R. C. 2003. A field guide to western reptiles and amphibians. 3rd ed. Houghton Mifflin Company.
- Steen, D. A. 2010. Snakes in the Grass: Secretive Natural Histories Defy Both Conventional and Progressive Statistics. *Herpetological Conservation and Biology* 5:183–188.
- Steen, D. A., C. J. W. McClure, J. C. Brock, D. Craig Rudolph, J. B. Pierce, J. R. Lee, W. Jeffrey Humphries, B. B. Gregory, W. B. Sutton, L. L. Smith, D. L. Baxley, D. J. Stevenson, and C. Guyer. 2014. Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions. S. Meiri, editor. *Journal of Animal Ecology* 83:286–295.
- Steen, D. A., L. L. Smith, L. M. Conner, J. C. Brock, and S. K. Hoss. 2007. Habitat Use of Sympatric Rattlesnake Species Within the Gulf Coastal Plain. *The Journal of Wildlife Management* 71:759–764.
- USFWS. 2014. Endangered and threatened wildlife and plants: Threatened status for the northern Mexican gartersnake and narrow-headed gartersnake, Final Rule. *Federal Register* 79:38677–38746.
- Waldron, J. L., S. H. Bennett, S. M. Welch, M. E. Dorcas, J. D. Lanham, and W. Kalinowsky. 2006. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. *Animal Conservation* 9:414–420.
- Waldron, J. L., S. M. Welch, S. H. Bennett, W. G. Kalinowsky, and T. A. Mousseau. 2013. Life history constraints contribute to the vulnerability of a declining North American rattlesnake. *Biological Conservation* 159:530–538.
- Webb, J. K., B. W. Brook, and R. Shine. 2002. What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecological Research* 17:59–67.

- Webb, J. K., B. W. Brook, and R. Shine. 2003. Does foraging mode influence life history traits? A comparative study of growth, maturation and survival of two species of sympatric snakes from south-eastern Australia. *Austral Ecology* 28:601–610.
- White, M., and J. A. Kolb. 1974. A Preliminary Study of *Thamnophis* near Sagehen Creek, California. *Copeia* 1974:126–136.
- Winne, C. T., J. D. Willson, K. M. Andrews, and R. N. Reed. 2006. Efficacy of Marking Snakes with Disposable Medical Cautery Units. *Herpetological Review* 37:52–54.
- Wood, D. A., I. D. Emmons, E. M. Nowak, B. L. Christman, A. T. Holycross, and A. G. Vandergast. 2018. Conservation Genomics of the Mogollon Narrow-Headed Gartersnake (*Thamnophis rufipunctatus*) and Northern Mexican Gartersnake (*Thamnophis eques megalops*). Open-File Report, Open-File Report, U.S. Geological Survey.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128.
- Wylie, G. D., J. J. Smith, M. Amarello, and Casazza, Michael L. 2011. A taping method for external transmitter Attachment on Aquatic Snakes. *Herpetological Review* 42:187–191.

Chapter 2: Conservation Translocation of *Thamnophis rufipunctatus*

Introduction

Biodiversity across the globe is declining at historical rates, and the need for adaptive strategies and active human intervention is vital for species conservation as anthropogenic and climate change threats increase (LeDee et al. 2021; Mawdsley et al. 2009). Many management strategies and tools are available to recover imperiled species including habitat protection and restoration, restoring connectivity, implementing sustainable take and reducing illegal take, and removing invasive species. However, these actions alone may often be insufficient to recover threatened and highly vulnerable species populations that have already declined. For example, in highly fragmented landscapes, semi- or impermeable barriers can restrict species movements among habitat patches thereby exacerbating threats to small populations and reducing the probability of natural recolonization from extirpated areas (Lande 1993; Parsons et al. 2010; Bastille-Rousseau and Wittemyer 2021). In these contexts, conservation translocations, where managers and practitioners assist the movement of organisms from one area to another, may be needed to enhance or reestablish populations within a species' native range (Griffith et al. 1989; Seddon et al. 2007; Germano et al. 2015).

Conservation translocations may employ a variety of release strategies including the use of wild-caught or captive-born individuals which can variously influence translocation success (Resende et al. 2020). Captive-born individuals have played an important role in the recovery of many imperiled species (Ralls and Ballou 2003; Santymire et al. 2014; Hill et al. 2018; Collar 2020; Pritchard et al. 2022). Captive-born individuals can be held and released at larger sizes (i.e., headstarting) which may result in greater post-release survival (Sacerdote-Velat et al. 2014). However, all captive-born individuals may still face issues from acclimation from captive to wild environments, disease, challenges with breeding in captivity, and the potential for lower

reproductive output following release, along with the potential for reduced genetic diversity due to genetic drift and increased susceptibility to climate change (Philippart 1995; Snyder et al. 1996; Araki et al. 2009; Bowkett 2009; McGinnity et al. 2009). Monitoring post-release success of captive-born translocated individuals is therefore critical to improving our understanding of how captive-born individuals can contribute towards recovery of wild species. Concurrent comparisons of post-release metrics (e.g., individual growth, movement, survival) on conspecific wild and captive-born individuals provide an excellent opportunity to provide this information.

The success of conservation translocation programs are influenced by a variety of factors therefore necessitating careful design (Batson et al. 2015). The diversity of species and contexts involved in conservation translocation may create challenges in identifying key themes to direct future translocation programs (Seddon et al. 2007). Nevertheless, some factors appear consistent in influencing translocation success, including incorporating species' life history and ecology into the program design and understanding and mitigating factors originally responsible for the species' decline (Bubac et al. 2019). The method by which individuals are released can also influence translocation success. Individuals released through a so-called hard release are simply released into their new environment without an acclimation phase (Griffith et al. 1989). Conversely, soft released individuals are given a means of on-site acclimation (e.g., outdoor pens, supplemental food) (Resende et al. 2021). Multiple reviews have found benefits to soft-releases such as reduced post-release dispersal movements and mortality (Fischer and Lindenmayer 2000; Massei et al. 2010; Resende et al. 2021).

Many translocation programs do not include post-release monitoring (Armstrong and Seddon 2008) or use short-term post-release monitoring (e.g., 1-4 years; Bubac et al. 2019) which further inhibits progress towards developing additional guidelines for conservation

translocation. Comparing sympatric or resident individuals to translocated individuals can provide an additional means for evaluating translocation success (Bauder et al. 2014). The best translocation outcomes, therefore, will likely come from multidisciplinary scientists in tandem with state and federal resource managers working together and incorporating experiments, models, and comparative analysis (Seddon et al. 2007).

Conservation programs often show taxonomic bias towards relatively large charismatic species (Seddon et al. 2005). For example, studies evaluating the success of conservation translocation for reptiles and amphibians were historically lacking compared to mammals and birds (Griffith et al. 1989; Dodd, Jr. and Seigel 1991). However, more recent reviews on amphibian and reptile conservation translocations report higher success rates (Germano and Bishop 2009). Although a scarcity of post-release monitoring for many reptile and amphibian translocation studies inhibits our understanding of factors influencing their relative success (Germano and Bishop 2009). Monitoring reptile and amphibian translocations is further complicated by their low detection rates and cryptic life histories which often makes it difficult to detect species using traditional survey or trapping methods (Steen 2010; Durso et al. 2011).

Here we set to evaluate the effectiveness of releasing zoo-born narrow-headed gartersnake (*Thamnophis rufipunctatus*), a federally threatened species, as part of a species recovery effort. Our release site was also the site of a concurrent monitoring study of wild resident narrow-headed gartersnakes and western terrestrial gartersnakes (*T. elegans*) which provided a unique opportunity to compare post-release behaviors of zoo-born gartersnakes with those of syntopic wild conspecifics and congeners. Our objectives were to compare the following metrics between wild and zoo-born narrow-headed gartersnakes: 1) encounters (i.e., catch) per unit effort using visual surveys and passive trapping, 2) movement patterns, 3) individual growth

rates, 4) apparent survival and recapture probabilities. We also compared these metrics between zoo-born gartersnakes released the same year (i.e., summer activity season) as their birth and zoo-born gartersnakes held one winter in captivity and released the following spring (i.e., headstarted).

Study site

The zoo-born gartersnakes used in this study were released at our monitoring site in Canyon Creek, Gila County, Arizona. Gartersnakes were released within our ca. 1.7 km survey reach of Canyon Creek (Fig. 2.1). The vegetation communities in and around Canyon Creek are described in Chapter 1 (Study site).

Methods

Zoo Managed Breeding Program

The Arizona Center for Nature Conservation/Phoenix Zoo (hereafter Zoo) formed an ex-situ breeding program for the narrow-headed gartersnake (hereafter THRU) during 2007 that was initiated by the Gartersnake Conservation Working Group due to marked declines in known populations of the species (Blais et al. 2022). This program was initially started with a founding population of seven individuals (three males and four females) from the Black River in central Arizona (Blais et al. 2022). The goals of this program included gaining additional knowledge of this species life history, reproductive ecology, feeding and behavioral ecology with the ultimate goal of producing zoo-born individuals to release into wild populations (Allard et al. 2018). Breeding efforts initially used common snake husbandry methods with induced brumation which led to copulations but no births and some health complications (Blais et al. 2022). Captive conditions were then modified to provide enclosures that mimicked natural refugia and

brumation cycles that resulted in successful offspring production and better overall adult health (Blais et al. 2022).

Prerelease Snake Processing

We marked all zoo-born snakes at the Zoo using subcutaneously injected visual implant elastomer (VIE, Chapter 1) as described by Major et al. (2020). We spaced injection sites 10 ventral scales apart along with using the right or left side of the individual and changed the VIE color each season which allowed for identification to each specific individual (e.g., R10 – R20 Yellow). Holdover snakes were also marked with a subcutaneously injected passive integrated transponder (PIT) tag at the Zoo using either a 9-digit 125kHz AVID (Avid Identification Systems, Inc., Norco, California) PIT tag (2023 holdovers) or a 134.2kHz Biomark (Boise, Idaho) APT12 PIT tag (2024 holdovers, Snakes recaptured in field). The former AVID encrypted PIT tags were not readable by the passive PIT tag array system deployed in May 2024 although one 2023 holdover THRU that was recaptured on 25 June 2024 was retagged with an APT12 PIT tag to allow it to be read by the passive arrays in the future.

Zoo to Wild Translocations

Zoo-born THRU from the Zoo's captive breeding program were released at Canyon Creek during four events from 2022–2024, totaling 54 snakes (Table 2.1). These releases included two cohorts of zoo-born snakes: two young-of-year (YOY) cohorts released the same year as their birth and two holdover cohorts that were held over the winter at the zoo and released the following spring. The first YOY release occurred 15 August 2022 where 24 THRU individuals born from three separate litters at the Zoo between 14 June 2022 and 18 July 2022 were released along with an

adult male that had been born at the Zoo 26 August 2019. The first holdover release occurred 9 June 2023 where 10 THRU born in 2022 from the same three litters as the 2022 YOY release were released on 9 June 2023. The second YOY release occurred on 17 August 2023 with 12 neonate THRU born on 11 August 2023 from the same litter. The second holdover release occurred on 14 May 2024 of seven THRU from a second litter born 29 August 2023. All zoo-born individuals were released between approximately 10:00 and 13:00 within approximately 2m from the edge of Canyon Creek (Fig. 2.1).

Field Surveys

Our field survey methodology is described in detail in Chapter 1 but is briefly described here. We performed multiple survey trips to Canyon Creek (hereafter sessions) during 2023 and 2024 where we used multiple sampling methods to capture/recapture gartersnakes: visual encounter surveys (VES), trapping with aquatic funnel traps, and/or passive PIT tag arrays. VES consisted of (2–7) surveyors walking the streamside and turning movable cover objects that were then replaced. We alternately began VES at each of our survey reach. We placed 35–111 Gee® minnow traps 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 with felt reducers along the stream bank per session and checked all traps twice per day. We baited traps with dead rainbow trout from the nearby Canyon Creek Fish Hatchery during most trapping sessions. During 2024 we deployed four passive PIT tag arrays that were operational from 14 May to 3 October 2024 as described in Chapter 1.

All data were collected and recorded in the same manner for zoo-born snakes including all processing and size information as in Chapter 1. We measured all captured snakes (snout vent

length [SVL] and tail length) by gently stretching the snake along a tape measure. We recorded each captured snake's weight and sex. We re-marked with PIT tags all recaptured zoo-born snakes that had been only previously marked with VIE.

Analysis

We used our VES data to calculate catch-per-unit-effort (CPUE) as the number of zoo-born THRU captured per session divided by the number of person-hrs standardized to captures per 100 person-hrs for each session. We calculated an overall VES CPUE of zoo-born THRU as the total number of captures divided by the total number of person-hrs 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 also calculated CPUE for zoo-born THRU captured by trapping per session as the number of captures divided by the number of trap-hrs standardized to captures per 100 trap-hs. We calculated a total trapping CPUE as described for the total VES CPUE. Finally, we calculated CPUE from the passive PIT tag arrays by first determining the total number of contacts by PIT-tagged zoo-born THRU at each array during each sampling session when PIT tag arrays were deployed. 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), that led to only including one contact per antenna-day. We then divided the number of contacts at each array during a given session by the number of hours that the array was deployed and converted these values to contacts per 100 antenna-hrs, and for the total combined contacts standardized as above across all sampling periods. We compared zoo-born THRU 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 evaluated changes in body size (SVL and weight) between consecutive recaptures between male and female gartersnakes and between wild THRU and our two zoo-born cohorts (YOY and holdover) using generalized linear mixed models (GLMM). Because our response variable (change in SVL or weight) was continuous and could be negative we used GLMM with gaussian error distributions and identity links. We included sex and cohort (wild, YOY, and holdover) 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 recaptures among individuals in each model as a continuous fixed-effect covariate. Smaller individuals may also show 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). The GLMM for change in SVL did not converge, presumably because of insufficient numbers of replicate measurements per snake (20 changes in SVL for 18 snakes) so we dropped the random effect of individual and instead fit a gaussian generalized linear model for change in SVL.

To evaluate gartersnake movement patterns and the extent to which those patterns may differ between wild THRU and among cohorts of zoo-born THRU, we first measured the Euclidean distance between consecutive gartersnake captures (both physical captures and PIT tag array detections). We then evaluated the effects of sex and cohort (wild, YOY, and holdover) 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 additive effects of cohort and 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 (L_{inf}), 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 (λ). 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 (L_{inf} , k , and λ) as additive functions of cohort (Wild, YOY, Holdover) and sex. Two neonate THRU (THRU10, THRU13) did not have SVL measurements on their initial capture in August 2022 but were both recaptured during 2023. To most fully 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 2.4) as necessary to ensure sufficient model convergence (c.f., Rose et al. 2018a, Chandler et al. 2023) while ensuring that our inferences were not sensitive to our choice of priors. 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 four 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, which could range from 0.50–1.0.

We used a Cormack-Jolly-Seber (CJS) model to estimate apparent survival (ϕ) and recapture probabilities (p) for wild THRU and each cohort of zoo-born THRU (YOY and holdover) (Cormack 1964; Jolly 1965; Seber 1965). The CJS model cannot distinguish between true survival and permanent emigration. Apparent survival rates may therefore underestimate true survival rates. We modeled 30-day apparent survival (ϕ_{30}) as an additive function of cohort and SVL. To account for potential changes in SVL during our study, particularly for small-bodied individuals, we used our Von Bertalanffy growth model to predict SVL for each individual at every capture occasion (i.e., session) 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. We modeled a constant 30-day apparent survival for wild THRU as we were not specifically interested in seasonal variation in survival. However, we were interested in how apparent survival changed over time for zoo-born THRU. We therefore estimated 30-day apparent survival separately for YOY and holdover snakes and for each cohort's first and second winter and first and second summer following release. To evaluate differences in sampling method efficacy between cohort, we modeled recapture probability as an interactive function between cohort and three types of sampling sessions. The first was what we refer to as Surveys and

included sessions employing VES and trapping (2022 and 2023; Table 2.1). The second was what we refer to as Surveys + Antenna and included VES/trapping sessions during 2024 where passive PIT tag arrays were also deployed. The third was what we refer to as Antenna and included sessions during 2024 where only passive PIT tag arrays were deployed. Some individuals were not marked with PIT tags (e.g., YOY snakes that were only marked with VIE upon release) and could therefore not be detected by passive PIT tag arrays. We therefore fixed recapture probability for Antenna sessions to zero for such individuals. We also estimated a separate recapture probability for sessions other than our formal survey sessions (e.g., trips focused on radio telemetry, releases of zoo-born THRU) that were pooled across cohort. Finally, we also estimate an additive effect of SVL on recapture probability but only for wild THRU 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. 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 ≤ 1.002 for all model parameters (Brooks and Gelman 1998; Gelman and Hill 2006).

Results

Post-release THRU Results

In total, we recaptured 19 zoo-born THRU representing individuals from all four release groups from 2022–2024, with number of recaptures ranging from 1 to 13 between all methods. We recaptured a higher proportion of individuals released from holdover (0.59) groups compared to YOY (0.25) groups (Tables 2.1). Physical recaptures (i.e., captures of zoo-born THRU made during VES, trapping, or incidental captures) led to a total of 23 recaptures among the 19 zoo-born individuals that were eventually recaptured (Table 2.2).

The number of person-hours per survey session ranged from 0 to 73.52 (mean = 54.25, SD = 28.15) and the number of trap-hours per survey session ranged from 0 to 17,928 (mean = 11,841, SD = 6,121) (Table 2.3). There was evidence that CPUE for VES (mean = 1.26 captures per 100 person-hrs; SD = 1.63) was more effective than trapping for recapturing zoo-born THRU (mean = 0.01 captures per 100 trap-hrs; SD = 0.01; $V = 3$, $P = 0.042$). Capture rates using passive PIT tag arrays (mean = 0.35 captures per 100 antenna-hrs; SD = 0.33) were higher than capture rates from trapping (mean = 0.01 captures per 100 trap-hrs; SD = 0.01; $t = 3.340$, $P = 0.007$). There was some evidence that capture rates from VES (mean = 1.26 captures per 100 person-hrs; SD = 1.63) were greater than capture rates using passive PIT tag arrays (mean = 0.35 captures per 100 antenna-hrs; SD = 0.33; $t = -1.972$, $P = 0.069$). Passive PIT tag arrays led to an additional 35 contacts from nine zoo-born individuals during 2024 (Table 2.1). Six of these nine individuals were only recaptured through PIT tag arrays and not through physical recaptures. We documented survival over one winter for seven individuals (Table 2.4). Five of these individuals were YOY released in 2022 and three of these five were also recaptured during 2024 documenting survival over two winters (Table 2.4).

Growth rate between wild and zoo-born THRU

We obtained 20 change (Δ) in SVL measurements from 18 THRU (five wild THRU, four holdover, nine YOY). Number of days between consecutive recaptures ranged from 23 to 369 days (median = 45 days) and SVL at first capture ranged from 202 to 521 mm (median = 231 mm). We found little evidence that changes in SVL between recaptures varied between wild (mean = $\Delta 77.60$ mm, SD = 86.13) and YOY zoo-born THRU (mean = $\Delta 73.36$ mm, SD = 76.23; $\beta_{\text{CohortYOY}} = -25.042$, $p = 0.161$) or holdover zoo-born THRU (mean = $\Delta 40.00$ mm, SD = 27.64; $\beta_{\text{CohortHoldover}} = 12.83$, $p = 0.583$) after controlling for initial SVL and time between recaptures. Change in SVL was also similar between sexes (males: mean = $\Delta 45.64$ mm, SD = 56.08; females: mean = $\Delta 94.78$ mm, SD = 79.51; $\beta_{\text{SexMALE}} = 6.337$, $p = 0.691$). We did find evidence of SVL at first capture ($\beta_{\text{First_SVL}} = -31.93$, $p = 0.002$) and time between recaptures ($\beta_{\text{Delta_Time}} = 64.06$, $p < 0.001$) both strongly influenced change in SVL.

We obtained 27 change (Δ) in weight measurements from 22 THRU (seven wild THRU, seven holdover, eight YOY). Number of days between consecutive recaptures ranged from 23 to 369 days (median = 28 days) and SVL at first capture ranged from 202 to 521 mm (median = 289 mm). There was little evidence that holdover THRU differed from wild THRU in their change in weight (wild: mean = $\Delta 9.29$ g, SD = 12.55; holdover: mean = $\Delta 8.31$ g, SD = 21.99; $\beta_{\text{CohortHoldover}} = 5.22$, $p = 0.354$) after controlling for initial weight and time between recaptures. However, YOY snakes tended to have less changes in weight compared to wild THRU (YOY: mean = $\Delta 7.06$ g, SD = 7.74; $\beta_{\text{CohortYOY}} = -9.12$, $p = 0.057$). Males also tended to have less change in weight (mean = $\Delta 3.11$ g, SD = 7.14) between recaptures than females (mean = $\Delta 13.38$ g, SD = 18.39; $\beta_{\text{SexMALE}} = -8.15$, $p = 0.038$). A snake's weight at first capture did not have a strong influence on subsequent change in weight ($\beta_{\text{Delta_Time}} = -2.08$, $P = 0.4256$) but time between recaptures did have a strong positive effect on change in weight ($\beta_{\text{Delta_Time}} = 11.30$, $P < 0.001$).

We used SVL measurements from 106 individuals (57 wild THRU, 37 YOY, and 12 holdovers) to fit our von Bertalanffy growth model. We had 16 individual THRU with more than one SVL measurement (eight wild THRU, six YOY, and two holdovers). Number of days between recaptures ranged from 23 to 369 days (median = 303 days). Our von Bertalanffy growth model indicated no strong evidence of variation between cohorts or sexes for asymptotic length or growth rate with the posterior probabilities for these parameters' coefficients being ≤ 0.81 (Table 2.5). There was weak evidence that YOY exhibited higher growth rates ($k_{YOY}=0.17$, 95%CRI = -0.23–0.58, PP=0.81) than wild THRU, and individual variation within YOY ($\lambda_{YOY}=51.58$, 95%CRI = -94.20–210.07, PP=0.75). There was some evidence that individual heterogeneity in growth rate was greater for males ($\lambda_{MALE} = 241.78$, 95%CRI = -66.50–722.83, PP = 0.91).

Movement

We had 71 measurements of Euclidean distance between consecutive recaptures across 41 individuals (22 wild THRU, nine YOY, 10 holdovers). Distances ranged from 3 to 672 m (median = 54 m) and the number of days between consecutive recaptures ranged from 0 to 711 days (median = 24 days). Holdover snakes moved further between consecutive recaptures (mean = 148 m, SD = 143) than wild snakes (mean = 77 m, SD = 122 m; $\beta_{Holdover} = 0.909$, $p= 0.017$) (Fig. 2.3). In contrast, YOY showed similar patterns of movement as wild THRU (mean = 63 m, SD = 61; $\beta_{YOY} = -0.066$, $p= 0.860$; Fig. 3). Males generally had similar distances between consecutive recaptures (mean = 111 m, SD = 128) as females (mean = 78 m, SD = 114; $\beta_{MALE} = 0.258$, $p=.403$). The furthest distance between consecutive recaptures was 672 m for holdover snakes, 602 m for wild snakes, and 205 m for YOY snakes (Fig. 2.4).

Apparent survival and recapture

We used mark-recapture data from 112 THRU (58 wild THRU, 36 YOY, 18 holdovers). Amongst individuals recaptured on at least one session (34 individuals), the median number of sessions with a recapture was two for wild THRU (maximum = six), four for YOY (maximum = nine), and three for holdovers (maximum = eight). Recapture probabilities were consistently higher for both cohorts of zoo-born THRU compared to wild THRU across all three session types (Survey, Survey + Antenna, Antenna; Table 2.6). Holdover snakes had the highest recapture probabilities during survey-based sessions ($p = 0.37\text{--}0.40$) followed by YOY snakes ($p = 0.21$) and wild snakes ($p = 0.09\text{--}0.14$; Table 2.6). All groups had relatively high recapture probabilities for antenna-only sessions ($p = 0.21\text{--}0.49$; Table 2.6). There was strong evidence that SVL was negatively related to recapture probability for wild THRU with larger snakes having lower recapture probabilities ($\beta = -0.80$, 95%CRI = $-1.67\text{--}0.03$, PP = 0.98).

The 30-day apparent survival for wild THRU across all seasons was 0.91 (95%CRI 0.86–0.96). There was weak evidence that SVL was negatively associated with apparent survival of wild THRU ($\beta = -0.17$, 95%CRI = $-0.64\text{--}0.27$, PP = 0.77). YOY had generally lower estimates of 30-day apparent survival that did not strongly vary among season ($\phi_{30} = 0.82\text{--}0.89$) and whose 95% CRI broadly overlapped. Holdover snakes had greater 30-day apparent survival over their first winter post-release ($\phi_{30} = 0.94$, 95% CRI = $0.80\text{--}0.99$) and lower 30-day apparent survival during summer although 95% CRI again broadly overlapped all estimates and were widest for holdover snakes (Table 2.6).

Discussion

Our post-release monitoring of zoo-born THRU released at Canyon Creek found multiple similarities in growth, movement, and apparent survival between zoo-born and resident wild THRU during two years of post-release monitoring. Most notably, our study documented post-release survival of zoo-born THRU across both one and two winters post-release. Our observations in the similarity of growth rates between wild and zoo-born THRU suggest that zoo-born snakes were able to forage successfully after release. This is further supported by observations of change in weight by zoo-born snakes over time. Four YOY snakes from the first release group in August 2022 showed consistent gains in weight when captured in the following active season during May through July 2023. All four of these snakes had more than doubled their weight and grew to lengths comparable to those of wild THRU recaptured over the same time period. Additionally, one holdover individual that was our only documented overwinter survival from this cohort (THRU21) doubled in mass (61.9 g to 129 g) over the 2023-2024 winter. This individual may also have been gravid when we recaptured her in 2024 although we could not confirm this.

Our estimates of movement and apparent survival were also similar between wild and YOY cohorts. While there was often substantial overlap in movement and apparent survival between wild THRU and holdover cohorts, holdover THRU did generally move further between recaptures and had lower apparent survival than wild THRU or YOY. We also did not detect a decline in apparent survival with increasing time since release. However, the uncertainty around our apparent survival estimates were relatively high for all groups making it difficult to draw firm conclusions about differences in post-release apparent survival among cohorts and over time. Nevertheless, our results collectively suggest that for the duration of our monitoring zoo-

born THRU released at Canyon Creek exhibited behaviors generally similar to those of wild-resident THRU.

Previous studies on gartersnake snake survival have reported higher survival rates for larger individuals (Hansen et al. 2015; Rose et al. 2018b) and higher survival rates for adults compared to juveniles (Bronikowski and Arnold 1999). We therefore expected holdover cohorts to have greater survival than YOY because they were released at larger body sizes. However, our data did not support this expectation with respect to apparent survival during the summer. Holdover snakes did move further between recaptures compared to YOY snakes and the maximum movement distance was also greater for holdover snakes. Furthermore, holdover snakes had higher recapture probabilities during survey sessions which may correspond to greater movement and/or surface activity. It is possible that greater movement and/or surface activity could have contributed to lower holdover survival. Our CJS model estimates apparent survival which does not distinguish between true survival and permanent emigration. It is therefore possible that greater movements by holdover snakes may have led to a higher degree of permanent emigration from our survey reach which would act to lower our estimates of apparent survival.

We found that VES was an effective survey method at Canyon Creek for wild and zoo-born THRU. Passive PIT tag arrays also resulted in many detections of zoo-born THRU and our highest recapture probabilities occurred during sessions employing only passive PIT tag arrays. Because our study was the first application, to our knowledge, of passive PIT tag arrays for monitoring aquatic snakes we specifically chose to place our arrays in areas with relatively high numbers of THRU captures during 2022 and 2023 in order to maximize the number of detections. This likely contributed to our high recapture probabilities by passive PIT tag arrays.

Additionally, these relatively high rates of detection and recapture by passive PIT tag arrays are likely due at least in part to the spatial proximity of the THRU release locations and our passive PIT tag arrays. Nevertheless, our results demonstrate the efficacy of this technology for monitoring aquatic snakes and highlights its potential for also monitoring post-release movement and survival of translocated aquatic snakes. However, one drawback for the use of this equipment is high initial cost, and limited streambank coverage based on antenna length. Another consideration is that snakes need to be large enough to receive a PIT tag to be detected by the arrays. Our YOY individuals were deemed too small to receive PIT tags and therefore could not be detected by passive PIT tag arrays unless they were recaptured and remarked with a PIT tag. Oldham et al. (2016) successfully PIT-tagged juvenile queen snakes (*Regina septemvittata*) as small as 2.4 g and 175 mm SVL suggesting that neonate gartersnakes could also be successfully PIT-tagged to increase the efficacy of monitoring using passive PIT tag arrays.

While we have demonstrated that the translocation of zoo-born THRU to the wild can be successful at the temporal extent examined in this study, we were unable to evaluate the extent to which these releases contributed to longer-term population dynamics of THRU at Canyon Creek. For example, we were unable to evaluate the reproductive success of zoo-born THRU or their degree of integration into the wild population. While this is difficult to do with the mark-recapture methods we employed this could be accomplished through genetic monitoring (Wood et al. 2018). Our results nevertheless illustrate the potential use of conservation translocation as a recovery tool for THRU. We encourage continued monitoring at Canyon Creek to document the long-term results of releasing zoo-born THRU. We also encourage future translocation studies of THRU and other imperiled snakes to integrate post-release monitoring of both translocated and

wild individuals at release sites to provide a reference for the post-release success of those translocations.

Figure 2.1. Map of release sites and survey reach for zoo-born *Thamnophis rufipunctatus* (THRU) along Canyon Creek, Arizona, during 2022–2024. Start and end points of typical surveys (visual encounter surveys and trapping), the locations of the four passive PIT tag arrays (numbered 1–4), and the four release sites for zoo-born THRU are presented. Zoo-born cohorts include young-of-year (YOY, released the same year of their birth) and holdover (Hold, held in captivity one winter following birth and released the following spring).

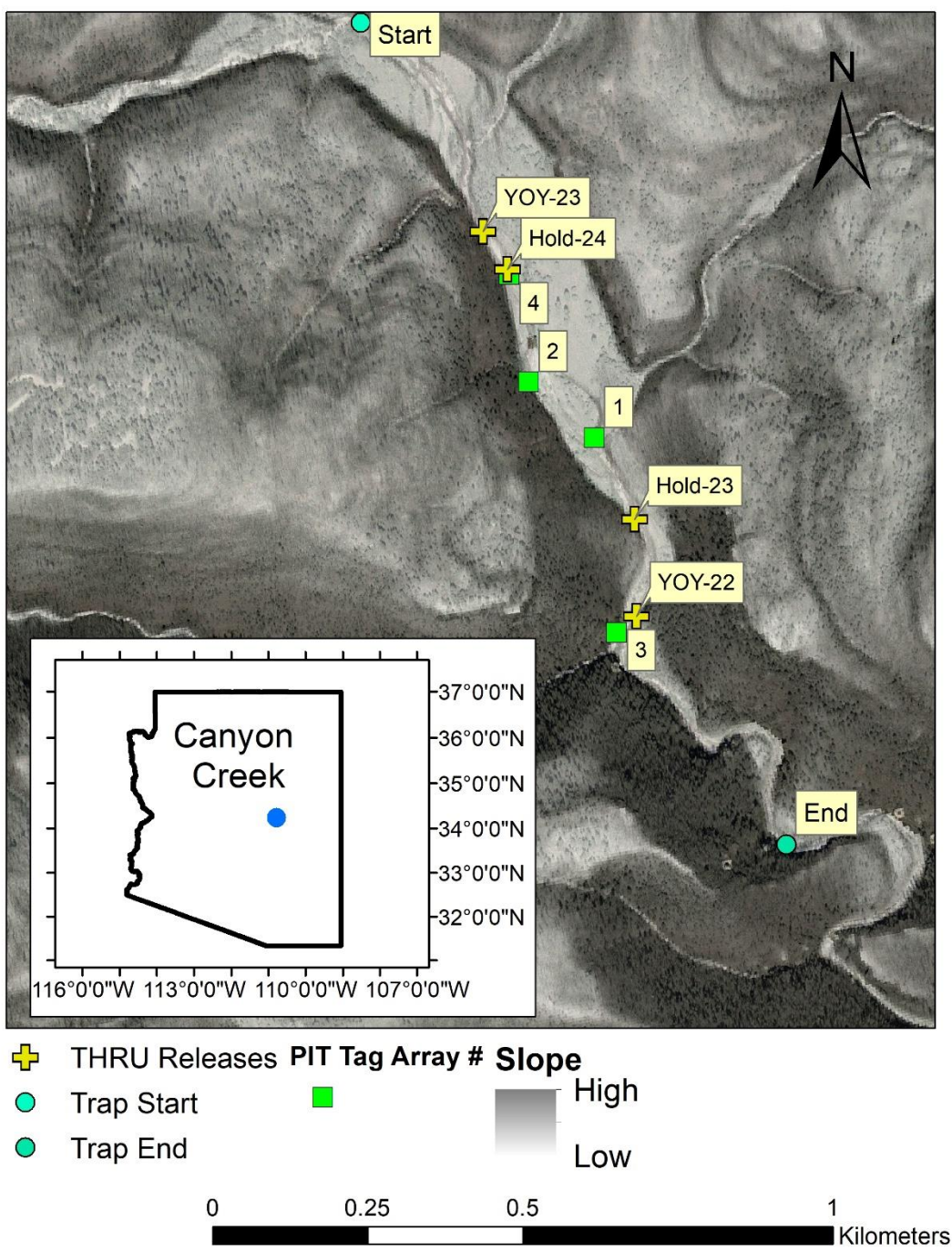


Table 2.1. Number of zoo-born *Thamnophis rufipunctatus* by released cohort born at the Phoenix Zoo and released at Canyon Creek, Arizona, during 2022–2024.

Year Born	Release Date	Cohort	Number of Individuals Released	Number of Individuals Recaptured	Proportion Recaptured
2022	Zoo Y1 August 15	YoY 1	25*	5	0.208
2023	Zoo H1 June 9	Holdover 1	10	5	0.5
2023	Zoo Y2 August 17	YoY 2	12	4	0.333
2024	Zoo H2 May 14	Holdover 2	7	5	0.714
Total			54	19	0.352

* Includes one 521 mm (snout vent length) adult that was in the Phoenix Zoo's breeding program since 26 August 2019.

Table 2.2. Survey and trapping effort and successes for zoo-born *Thamnophis rufipunctatus* (THRU) released from the Phoenix Zoo at Canyon Creek, Arizona, during 2022–2024. Trip types include Trap (combination of visual encounter surveys and trapping) and Track (trips focused on radio telemetry of wild gartersnakes). Incidental captures were made outside of formal survey sessions.

Year	Trip	Number of Traps	Trap Nights	Trap Hours	VES hours	VES	Trap	Incidental	THRU Total	THRU / 100 VES hours	THRU / 100 Trap hours
2023	Trap 1 May (24-30)*	85	506	12144	67.62	0	1	0	1	0.000	0.008
2023	Track 1 June (6-9)*	50	147	3528	27.90	0	0	0	0	0.000	0.000
2023	Track 2 June (12-15)	0	NA	NA	37.65	2	0	0	2	5.312	NA
2023	Trap 2 June (21-28)*	100	694	16656	84.10	0	4	0	4	0.000	0.024
2023	Trap 3 July (19-26)*	102	687	16488	72.90	2	4	0	6	2.743	0.024
2023	Track 5 August (1-3)	0	NA	NA	6.03	0	0	0	0	0.000	NA
2023	Trap 4 August (16-23)*	108	747	17928	91.60	1	3	1	5	1.092	0.017
2023	TOTALS	445	2781	66744	387.80	5	12	1	18	1.289	0.018
2024	Trap 5 May (22-26)	111	479.5	11508	63.33	2	0	0	2	3.158	0.000
2024	Trap 6 June (19-26)*	105	735	17640	73.52	1	2	0	3	1.360	0.011
2024	Trap 7 July (17-20)*	110	385	9240	54.72	0	0	0	0	0.000	0.000
2024	Trap 8 August (19-20)*	40	60	1440	17.37	0	0	0	0	0.000	0.000
	TOTALS	366	1659.5	39828	208.94	3	2	0	5	1.436	0.005
2023-2024	Combined TOTALS	811	4440.5	106572	596.75	8	14	1	23	1.341	0.013

Table 2.3. Detections of zoo-born *Thamnophis rufipunctatus* (THRU) born at the Phoenix Zoo and released at Canyon Creek, Arizona, during 2022–2024 by four passive PIT (passive integrated transponder) tag arrays during 2024. Hours deployed is the cumulative number of hours during each session that arrays were on and scanning for PIT-tagged snakes. Trip types include Trip types include Trap (combination of visual encounter surveys, trapping, and passive PIT tag arrays) and Ant (only passive PIT tag arrays). 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.

Year	Trip	Cumulative Hours Deployed	THRU Contacts*	THRU Unique**	THRU / 100 hours
2024	Ant 1 May (14-21)	434	1	1	0.230
2024	Trap 5 May (22-26)	358	1	1	0.279
2024	Ant 2 May 27 - June 18	1642	10	6	0.609
2024	Trap 6 June (19-26)	572	7	4	1.224
2024	Ant 3 June 27 - July 16	1455	4	3	0.275
2024	Trap 7 July (17-20)	269	1	1	0.372
2024	Ant 4 July 21 - August 18	1699	5	3	0.294
2024	Trap 8 August (19-20)	148	0	0	0.000
2024	Ant 5 August 21 - September 5	1152	4	3	0.347
2024	Ant 6 September (6-20)	1065	0	0	0.000
2024	Ant 7 September 21 - October 3	1010	2	2	0.198
TOTALS		9804	35	9***	0.357

Figure 2.2. Detections of zoo-born *Thamnophis rufipunctatus* (THRU) born at the Phoenix Zoo and released at Canyon Creek, Arizona, during 2022–2024 by four passive PIT (passive integrated transponder) tag arrays by survey trip during 2024.

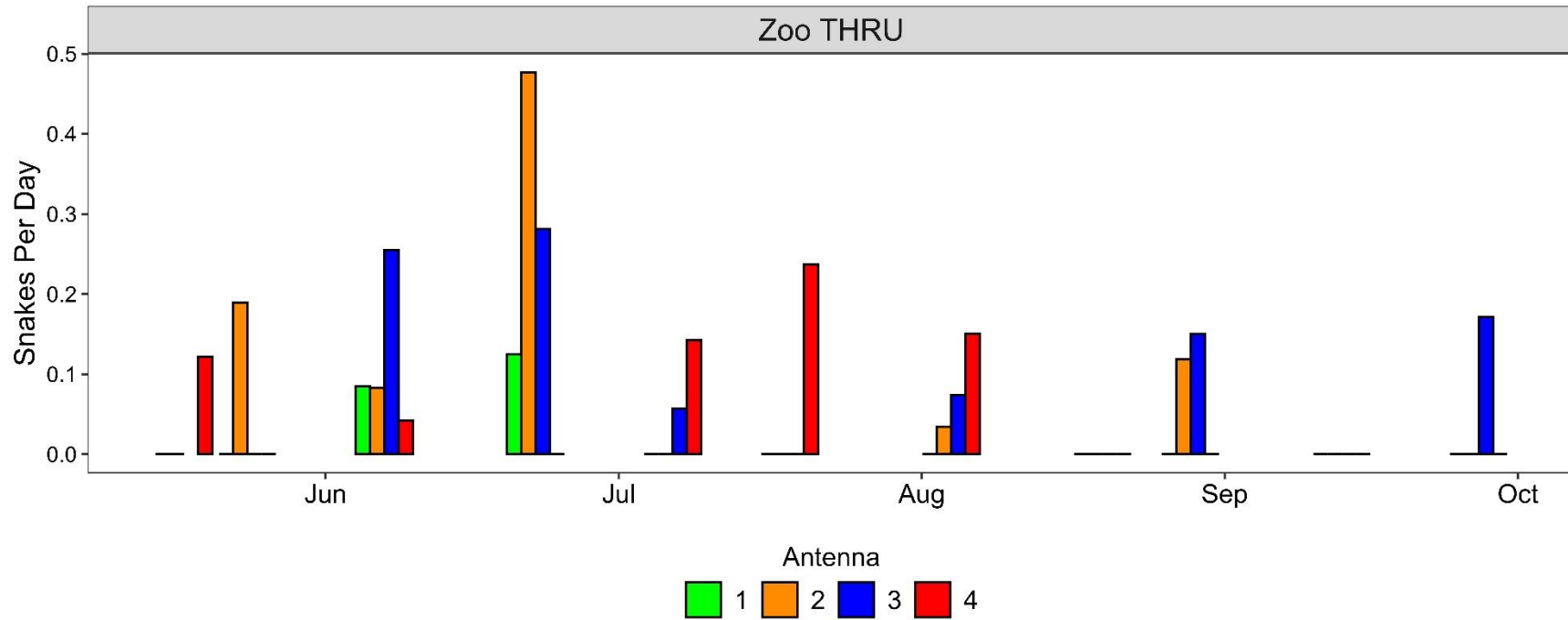


Table 2.4. Recapture information for zoo-born *Thamnophis rufipunctatus* (THRU) born at the Phoenix Zoo and released at Canyon Creek, Arizona, during 2022–2024 that were recaptured at least once during this study. Cohorts are young-of-year (YOY) or holdover (released the spring following their birth the previous summer). Active and passive recaptures (recap) indicates captures from VES, trapping, or incidental (active) and Antenna contacts (passive). Recapture methods include visual encounter surveys (VES), aquatic funnel traps (Trap), passive PIT tag array (Ant), and incidental captures made outside of formal surveys (Incidental). Survived first and second winters denote individuals that were (X) or were not (-) recaptured one or two winters following their release.

Snake ID	Cohort	Release Date	Sex	SVL (mm)	Mass (g)	Active Recap	Passive Recap	Recapture Method	Survived First Winter	Survived Second Winter
THRU35	YOY	15-Aug-22	M	230	7	1	2	VES,Ant	X	X
THRU1	YOY	15-Aug-22	F	220	8	3	10	VES,Trap,Ant	X	X
THRU37	YOY	15-Aug-22	M	220	7	1	2	Trap,Ant	X	X
THRU18	YOY	15-Aug-22	F	215	6	2	0	VES,Trap	X	-
THRU26	YOY	15-Aug-22	M	521	77	1	NA	Trap	X	-
THRU24	HO	9-Jun-23	M	NA	38.1	1	NA	Trap	-	NA
THRU40	HO	9-Jun-23	M	NA	45.1	1	NA	Trap	-	NA
THRU16	HO	9-Jun-23	F	NA	48.9	1	NA	VES	-	NA
THRU21	HO	9-Jun-23	F	NA	61.9	2	0	VES,Trap	X	NA
THRU38	HO	9-Jun-23	M	NA	42.8	2	NA	VES,Trap	-	NA
THRU48	YOY	17-Aug-23	F	214	4.3	1	NA	Trap	-	NA
THRU49	YOY	17-Aug-23	M	213	4.7	1	NA	Trap	-	NA
THRU51	YOY	17-Aug-23	F	226	4.9	2	2	Trap,Ant,Incidental	X	NA
THRU61	YOY	17-Aug-23	M	202	3.1	1	NA	Trap	-	NA
THRU71	HO	14-May-24	F	370	32.8	0	4	Ant	NA	NA
THRU63	HO	14-May-24	M	365	32.7	1	1	VES,Ant	NA	NA
THRU69	HO	14-May-24	M	370	30.8	1	1	Trap,Ant	NA	NA
THRU65	HO	14-May-24	M	345	22.7	1	3	VES,Ant	NA	NA
THRU70	HO	14-May-24	M	365	29.1	0	10	Ant	NA	NA

Table 2.5. 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 wild and zoo-born *Thamnophis rufipunctatus* at Canyon Creek, Arizona, during 2022–2024. Zoo-born snakes were represented in two cohorts: young-of-year (YOY) and holdover. 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,)	0.692	0.572	0.856	1
Annual growth rate	k	Normal(1,0.316)T(0,)	1.039	0.638	1.513	1
Annual growth rate	k(YOY)	Normal(0,0.316)	0.172	-0.232	0.58	0.806
Annual growth rate	k(Holdover)	Normal(0,0.316)	0.061	-0.467	0.624	0.578
Annual growth rate	k(Male)	Normal(0,0.316)	0.048	-0.342	0.475	0.584
Individual variation	lambda	Normal(150,100)	120.738	27.953	280.009	1
Individual variation	lambda(YOY)	Normal(0,100)	51.582	-94.199	210.066	0.747
Individual variation	lambda(Holdover)	Normal(0,100)	43.035	-108.622	214.938	0.686
Individual variation	lambda(Male)	Normal(0,316.228)	241.782	-66.497	722.83	0.905
Measurement error	sd.eps	Uniform(0,0.5)	0.012	0.002	0.027	1

Table 2.6. 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 wild and zoo-born *Thamnophis rufipunctatus* (THRU) at Canyon Creek, Arizona, during 2022–2024. Model parameters include recapture probability (p) and 30-day apparent survival (ϕ). Surveys are sessions used both visual encounter surveys 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 cohorts. $\beta(\text{SVL})$ is the slope estimate for an additive effect of SVL as a time-varying individual covariate on for both p and ϕ predicted from our 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	Wild Survey + Antenna	Beta (1,1)	0.087	0.021	0.209	1
Recapture	YOY Survey + Antenna	Beta (1,1)	0.209	0.056	0.443	1
Recapture	Holdover Survey + Antenna	Beta (1,1)	0.401	0.196	0.636	1
Recapture	Wild Survey	Beta (1,1)	0.14	0.064	0.246	1
Recapture	YOY Survey	Beta (1,1)	0.205	0.066	0.412	1
Recapture	Holdover Survey	Beta (1,1)	0.365	0.161	0.614	1
Recapture	Wild Antenna	Beta (1,1)	0.214	0.11	0.346	1
Recapture	YOY Antenna	Beta (1,1)	0.493	0.273	0.718	1
Recapture	Holdover Antenna	Beta (1,1)	0.434	0.23	0.659	1
Recapture	Other Session	Beta (1,1)	0.041	0.011	0.09	1
Recapture	$\beta(\text{SVL})$ - Wild	Normal (0,1.648)	-0.796	-1.672	-0.034	0.98
Survival	$\beta(\text{SVL})$ - Wild	Normal (0,1.648)	-0.165	-0.643	0.265	0.768
Survival	Wild ϕ	Beta (1,1)	0.913	0.861	0.962	1
Survival	YOY ϕ Winter 1	Beta (1,1)	0.886	0.791	0.973	1
Survival	YOY ϕ Winter 2	Beta (1,1)	0.816	0.294	0.998	1
Survival	YOY ϕ Summer 1	Beta (1,1)	0.814	0.291	0.997	1
Survival	YOY ϕ Summer 2	Beta (1,1)	0.854	0.619	0.988	1
Survival	Holdover ϕ Winter 1	Beta (1,1)	0.936	0.798	0.998	1
Survival	Holdover ϕ Summer 1	Beta (1,1)	0.495	0.025	0.972	1
Survival	Holdover ϕ Summer 2	Beta (1,1)	0.5	0.103	0.914	1

Figure 2.3. Predicted Euclidian distances (m) between consecutive recaptures with 95% confidence intervals (CI) for wild and zoo-born *Thamnophis rufipunctatus* at Canyon Creek, Arizona during 2023–2024. Zoo-born snakes were released in two cohorts: young-of-year (YOY) and holdover.

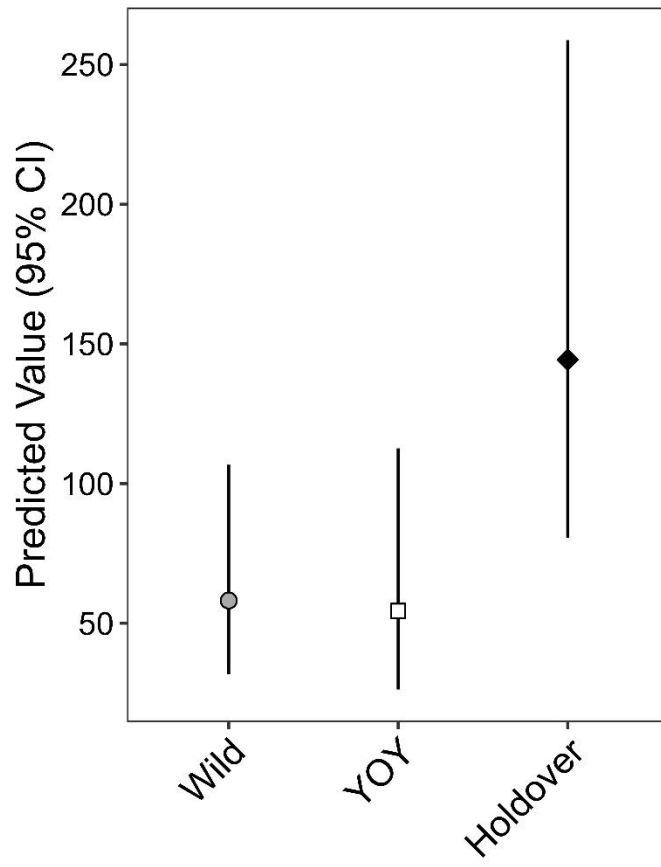


Figure 2.4. Histogram of Euclidian distance (m) between consecutive recaptures for wild and zoo-born *Thamnophis rufipunctatus* at Canyon Creek, Arizona during 2022–2024. Zoo-born snakes were released as two cohorts: young-of-year (YOY) and holdover.



Literature cited

- Allard, Ruth.A., Scott.A. Wells, B.A. Minter, J. Maienschein, and J.P. Collins. 2018. The Phoenix Zoo Story: Building a legacy of conservation. Pp. 169–177 in *The Ark and Beyond: The Evolution of Zoo and Aquarium Conservation*. University of Chicago Press.
- Araki, H., B. Cooper, and M.S. Blouin. 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biol. Lett.* 5:621–624. DOI: <https://doi.org/10.1098/rsbl.2009.0315>
- Armstrong, D., and P. Seddon. 2008. Directions in reintroduction biology. *Trends in Ecology & Evolution* 23:20–25. DOI: <https://doi.org/10.1016/j.tree.2007.10.003>
- Bastille-Rousseau, G., and G. Wittemyer. 2021. Characterizing the landscape of movement to identify critical wildlife habitat and corridors. *Conservation Biology* 35:346–359. DOI: <https://doi.org/10.1111/cobi.13519>
- Batson, W.G., I.J. Gordon, D.B. Fletcher, and A.D. Manning. 2015. Translocation tactics: a framework to support the IUCN Guidelines for wildlife translocations and improve the quality of applied methods. *Journal of Applied Ecology* 52:1598–1607. DOI: <https://doi.org/10.1111/1365-2664.12498>
- Bauder, J.M., C. Castellano, J.B. Jensen, D.J. Stevenson, and C.L. Jenkins. 2014. Comparison of movements, body weight, and habitat selection between translocated and resident gopher tortoises: Gopher Tortoise Translocation. *Jour. Wild. Mgmt.* 78:1444–1455. DOI: <https://doi.org/10.1002/jwmg.790>
- Blais, B.R., S.A. Wells, B.M. Poynter, J.L. Koprowski, M.M. Garner, and R.A. Allard. 2022. Adaptive management in a conservation breeding program: Mimicking habitat complexities facilitates reproductive success in narrow-headed gartersnakes (*Thamnophis rufipunctatus*). *Zoo Biology* 41:346–353. DOI: <https://doi.org/10.1002/zoo.21682>
- Bowkett, A.E. 2009. Recent Captive-Breeding Proposals and the Return of the Ark Concept to Global Species Conservation. *Conservation Biology* 23:773–776. DOI: <https://doi.org/10.1111/j.1523-1739.2008.01157.x>
- Bronikowski, A.M., and S.J. Arnold. 1999. The Evolutionary Ecology of Life History Variation in the Garter Snake *Thamnophis Elegans*. *Ecology* 80:2314–2325. DOI: [https://doi.org/10.1890/0012-9658\(1999\)080\[2314:TEEOLH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2314:TEEOLH]2.0.CO;2)

- Brooks, M., E., K. Kristensen, K. Benthem J., van, A. Magnusson, C. Berg W., A. Nielsen, H. Skaug J., M. Mächler, and B. Bolker M. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9:378. DOI: <https://doi.org/10.32614/RJ-2017-066>
- Brooks, S.P., and A. Gelman. 1998. General Methods for Monitoring Convergence of Iterative Simulations. *Journal of Computational and Graphical Statistics* 7:434–455. DOI: <https://doi.org/10.1080/10618600.1998.10474787>
- Bubac, C.M., A.C. Johnson, J.A. Fox, and C.I. Cullingham. 2019. Conservation translocations and post-release monitoring: Identifying trends in failures, biases, and challenges from around the world. *Biological Conservation* 238:108239. DOI: <https://doi.org/10.1016/j.biocon.2019.108239>
- Chandler, H.C., D. Steen, J. Blue, ... J.M. Bauder. 2023. Evaluating Growth Rates of Captive, Wild, and Reintroduced Populations of the Imperiled Eastern Indigo Snake (*Drymarchon couperi*). *Herpetologica* 79. DOI: <https://doi.org/10.1655/Herpetologica-D-22-00041>
- Collar, N.J. 2020. Preparing captive-bred birds for reintroduction: the case of the Vietnam Pheasant *Lophura edwardsi*. *Bird Conservation International* 30:559–574. DOI: <https://doi.org/10.1017/S0959270920000039>
- Cormack, R.M. 1964. Estimates of Survival from the Sighting of Marked Animals. *Biometrika* 51:429–438.
- Dodd, Jr., C.K., and R.A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? *Herpetologica* 47:336–350. DOI: [https://doi.org/10.1016/0006-3207\(92\)91063-X](https://doi.org/10.1016/0006-3207(92)91063-X)
- Durso, A.M., J.D. Willson, and C.T. Winne. 2011. Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation* 144:1508–1515. DOI: <https://doi.org/10.1016/j.biocon.2011.01.020>
- Eaton, M.J., and W.A. Link. 2011. Estimating age from recapture data: integrating incremental growth measures with ancillary data to infer age-at-length. *Ecological Applications* 21:2487–2497. DOI: <https://doi.org/10.1890/10-0626.1>
- Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265–289.

- Fischer, J., and D.B. Lindenmayer. 2000. An assessment of the published results of animal relocations. *Biological Conservation* 96:1–11. DOI: [https://doi.org/10.1016/S0006-3207\(00\)00048-3](https://doi.org/10.1016/S0006-3207(00)00048-3)
- Gelman, A., and J. Hill. 2006. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, New York.
- Germano, J.M., and P.J. Bishop. 2009. Suitability of Amphibians and Reptiles for Translocation. *Conservation Biology* 23:7–15. DOI: <https://doi.org/10.1111/j.1523-1739.2008.01123.x>
- Germano, J.M., K.J. Field, R.A. Griffiths, S. Clulow, J. Foster, G. Harding, and R.R. Swaisgood. 2015. Mitigation-driven translocations: are we moving wildlife in the right direction? *Frontiers in Ecol & Environ* 13:100–105. DOI: <https://doi.org/10.1890/140137>
- Griffith, B., M.J. Scott, J.W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.
- Hansen, E.C., R.D. Scherer, G.C. White, B.G. Dickson, and E. Fleishman. 2015. Estimates of Survival Probability from Two Populations of Giant Gartersnakes in California’s Great Central Valley. *Copeia* 103:1026–1036. DOI: <https://doi.org/10.1643/CE-15-233>
- Hill, R., A. Coetsee, and D. Sutherland. 2018. Recovery of the mainland subspecies of eastern barred bandicoot. Pp. 249 in *Recovering Australian Threatened Species: A Book of Hope* (S. Garnett, J. Woinarski, D. Lindenmayer, and P. Latch, eds.). Csiro Publishing.
- Jolly, G.M. 1965. Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. *Biometrika* 52:225–247.
- Kellner, K. 2015. jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses. CRAN: Contributed Packages DOI: <https://doi.org/10.32614/cran.package.jagsui>
- Lande, R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. *The American Naturalist* 142:911–927. DOI: <https://doi.org/10.1086/285580>
- LeDee, O.E., S.D. Handler, C.L. Hoving, C.W. Swanston, and B. Zuckerberg. 2021. Preparing Wildlife for Climate Change: How Far Have We Come? *J Wildl Manag* 85:7–16. DOI: <https://doi.org/10.1002/jwmg.21969>

- Major, T., D.R. Atkins, L. Jeffrey, and W. Wüster. 2020. Marking the un-markable: visible implant elastomer in wild juvenile snakes. *HJ* 173–176. DOI: <https://doi.org/10.33256/hj30.3.173176>
- Massei, G., R.J. Quyy, J. Gurney, and D.P. Cowan. 2010. Can translocations be used to mitigate human–wildlife conflicts? *Wildl. Res.* 37:428–439. DOI: <https://doi.org/10.1071/WR08179>
- Mawdsley, J.R., R. O’Malley, and D.S. Ojima. 2009. A Review of Climate-Change Adaptation Strategies for Wildlife Management and Biodiversity Conservation. *Conservation Biology* 23:1080–1089. DOI: <https://doi.org/10.1111/j.1523-1739.2009.01264.x>
- McGinnity, P., E. Jennings, E. deEyto, N. Allott, P. Samuelsson, G. Rogan, K. Whelan, and T. Cross. 2009. Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. *Proc. R. Soc. B.* 276:3601–3610. DOI: <https://doi.org/10.1098/rspb.2009.0799>
- Parsons, T.L., C. Quince, and J.B. Plotkin. 2010. Some Consequences of Demographic Stochasticity in Population Genetics. *Genetics* 185:1345–1354. DOI: <https://doi.org/10.1534/genetics.110.115030>
- Philippart, J.C. 1995. Is captive breeding an effective solution for the preservation of endemic species? *Biological Conservation* 72:281–295. DOI: [https://doi.org/10.1016/0006-3207\(94\)00090-D](https://doi.org/10.1016/0006-3207(94)00090-D)
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*
- Pritchard, R.A., E.L. Kelly, J.R. Biggs, A.N. Everaardt, R. Loyn, M.J.L. Magrath, P. Menkhorst, C.J. Hogg, and W.L. Geary. 2022. Identifying cost-effective recovery actions for a critically endangered species. *Conservat Sci and Prac* 4:e546. DOI: <https://doi.org/10.1111/csp2.546>
- R Core Team. 2024. R: A language and environment for statistical computing. <<<https://www.R-project.org/>>>.
- Ralls, K., and J.D. Ballou. 2003. Genetic Status and Management of California Condors. *The Condor* 106:215–228.

- Resende, P.S., A.B. Viana-Junior, R.J. Young, and C.S. Azevedo. 2021. What is better for animal conservation translocation programmes: Soft- or hard-release? A phylogenetic meta-analytical approach. *Journal of Applied Ecology* 58:1122–1132. DOI: <https://doi.org/10.1111/1365-2664.13873>
- Resende, P.S., A.B. Viana–Junior, R.J. Young, and C.S.D. Azevedo. 2020. A global review of animal translocation programs. *Anim. Biodiv. Conserv.* 221–232. DOI: <https://doi.org/10.32800/abc.2020.43.0221>
- Rose, J.P., B.J. Halstead, G.D. Wylie, and M.L. Casazza. 2018a. Spatial and Temporal Variability in Growth of Giant Gartersnakes: Plasticity, Precipitation, and Prey. *Journal of Herpetology* 52:40–49. DOI: <https://doi.org/10.1670/17-055>
- Rose, J.P., G.D. Wylie, M.L. Casazza, and B.J. Halstead. 2018b. Integrating growth and capture–mark–recapture models reveals size-dependent survival in an elusive species. *Ecosphere* 9:e02384. DOI: <https://doi.org/10.1002/ecs2.2384>
- Sacerdote-Velat, A.B., J.M. Earnhardt, D. Mulkerin, D. Boehm, and G. Glowacki. 2014. Evaluation of headstarting and release techniques for population augmentation and reintroduction of the smooth green snake. *Animal Conservation* 17:65–73. DOI: <https://doi.org/10.1111/acv.12151>
- Santymire, R.M., T.M. Livieri, H. Branvold-Faber, and P.E. Marinari. 2014. The black-footed ferret: on the brink of recovery? Pp. 119–134 in *Reproductive Sciences in Animal Conservation: Progress and Prospects* (W.V. Holt, J.L. Brown, and P. Comizzoli, eds.). Springer New York, New York, NY.
- Seber, G.A.F. 1965. A Note on the Multiple-Recapture Census. *Biometrika* 52:249–259.
- Seddon, P.J., D.P. Armstrong, and R.F. Maloney. 2007. Developing the Science of Reintroduction Biology. *Conservation Biology* 21:303–312. DOI: <https://doi.org/10.1111/j.1523-1739.2006.00627.x>
- Seddon, P.J., P.S. Soorae, and F. Launay. 2005. Taxonomic bias in reintroduction projects. *Animal Conservation* 8:51–58. DOI: <https://doi.org/10.1017/S1367943004001799>
- Snyder, N.F.R., S.R. Derrickson, S.R. Beissinger, J.W. Wiley, T.B. Smith, W.D. Toone, and B. Miller. 1996. Limitations of Captive Breeding in Endangered Species Recovery. *Conservation Biology* 10:338–348. DOI: <https://doi.org/10.1046/j.1523-1739.1996.10020338.x>

Steen, D.A. 2010. Snakes in the Grass: Secretive Natural Histories Defy Both Conventional and Progressive Statistics. *Herpetological Conservation and Biology* 5:183–188.

Wood, D.A., I.D. Emmons, E.M. Nowak, B.L. Christman, A.T. Holycross, and A.G. Vandergast. 2018. Conservation Genomics of the Mogollon Narrow-Headed Gatersnake (*Thamnophis rufipunctatus*) and Northern Mexican Gartersnake (*Thamnophis eques megalops*). U.S. Geological Survey.