POPULATION ECOLOGY OF NORTHERN MEXICAN GARTERSNAKES (*Thamnophis eques megalops*) AT BUBBLING PONDS HATCHERY COMPLEX

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EXECUTIVE SUMMARY

Once widespread and abundant in riparian areas and wetlands throughout central and southern Arizona, Northern Mexican Gartersnakes (*Thamnophis eques megalops*) have declined and now persist in only a fraction of their former distribution. Because of their declines the species was listed as Threatened under the Endangered Species Act of 1973 in 2014. Mexican Gartersnakes are also Tier 1A Species of Greatest Conservation Need in Arizona's State Wildlife Action Plan. There are currently only a few isolated populations where the species is still commonly found in the middle/upper Verde River drainage, middle/lower Tonto Creek, the Bill Williams River drainage, upper Santa Cruz River drainages, and Ciénega Creek drainage. The Arizona Game and Fish Department fish hatcheries at Page Springs and Bubbling Ponds, in the Verde River drainage, support one of the largest known Northern Mexican Gartersnake populations in Arizona. Understanding the population dynamics of this population is important to shed light on the species ecology and to inform how hatchery management can benefit the species. From 2009–2011 the Department conducted a five-year mark-recapture study to assess relative abundance, detection, population dynamics, and the natural history of the Northern Mexican Gartersnake at the Page Springs and Bubbling Ponds hatcheries. In 9,510 trap days over five-years a total of 237 were captured and 188 marked in annual surveys done from May–September. Annual relative abundance, detection, and size class distribution exhibited little variation suggesting a stable population. We found snakes to be most abundant around ponds from June to August and didn't vary between fallow and unlined ponds. Sex ratios were strongly female biased and few young and subadult snakes were captured, but these biases are suspected to be related to the trapping technique and not an inherent aspect of the population structure. Despite coexisting with a large population of the non-native and predatory America Bullfrog (*Rana catesbeiana*) we found no evidence that tail injuries in this population are higher than populations without American Bullfrogs. This study provides a baseline on the Northern Mexican Gartersnake population at the Page Springs and Bubbling Ponds hatcheries to assess future trends and changes and guide the timing of maintenance around ponds.

INTRODUCTION

In many environments snakes are species rich and abundant, yet their secretive habits and low encounter and detection rates often make them difficult to study (Steen 2010; Durso and Seigel 2015). For instance, low detection rates can underestimate geographic ranges (Kéry 2002), produce unreliable abundance (Lind et al. 2005; McCarthy et al. 2013) and inaccurate detection probability estimates, even when using robust algorithm-based statistical techniques (Royle and Nichols 2003; Steen et al. 2012). Consequently, there are significant gaps in the basic ecology, population demography and dynamics, and population trends for most snake species, which can hinder conservation assessments and management strategies (Dorcas and Willson 2009; Durso et al. 2011). Dealing with low capture rates can be daunting, but using long-term mark-recapture can help estimate demographic parameters (i.e., growth rates, survivorship, population size), identify vulnerable life stages, and determine underlying mechanisms that govern population dynamics (Lind et al. 2005; Mazerolle et al. 2007; Lindenmayer and Likens 2009; McDiarmid et al. 2012). This information is especially needed and valuable for the management and recovery of species of conservation concern.

The northern Mexican gartersnake (*Thamnophis eques megalops*; *T. eques* hereafter) fits the profile of a rare elusive species of conservation concern for which we lack basic demography, population dynamics, and life history information. This semi-aquatic snake has declined throughout the United States and has been listed as Threatened under the Endangered Species Act (USFWS 2014) and as a Tier 1A Species of Greatest Conservation Need in Arizona's State Wildlife Action Plan (AZGFD 2012). Once widespread and relatively abundant in aquatic habitats between 50–1875 m elevation in central and southern Arizona, *T. eques* is now restricted to localized populations along the middle/upper Verde River drainage, middle/lower Tonto Creek, Bill Williams River system, upper Santa Cruz and San Pedro river drainages, and a few isolated wetlands (Rosen and Schwalbe 1988; Holycross et al. 2006; Jones et al. in press). Primary threats and contributors to the decline of the species include modification of riparian and aquatic habitats from water diversions, habitat loss, loss of native prey, and competition and predation by nonnative species (Jennings and Hayes 1994; Rosen and Schwalbe 1988; Clarkson and Rorabaugh 1989; Holm and Lowe 1995; USFWS 2014). Because of its protected status, it is incumbent on Arizona Game and Fish Department (AZGD) to understand the fundamental ecology, assess threats, and study sampling methods to increase detection, all of which will help forge a sound conservation and recovery plan, for *T. eques*.

One ideal location for a long-term autecological study of *T. eques* is Bubbling Ponds Fish Hatchery (BPFH), comprising Page Springs and Bubbling Ponds hatcheries, located in central Arizona, because it supports one of the largest known *T. eques* populations in the United States (USFWS 2014). BPFH is a multi-use facility that balances fish production and public recreation while actively managing a threatened snake species. The hatchery is managed by AZGD for native and nonnative fish production, and also supports a large population of the nonnative and invasive *Rana catesbeiana* (American bullfrog, referred to as bullfrog hereafter). Because of fish production activities, key resources for *T. eques* are stable, including water levels, as well as fish and amphibians, upon both of which *T. eques* readily preys (Emmons et al. 2016). The combination of high snake abundance, presence of problematic invasive species, and stable resources at BPFH provides the opportunity to elucidate basic population properties of *T. eques*, and the species' direct or indirect interactions with nonnative species.

To date, two telemetry studies have investigated habitat use, seasonal activity patterns, and movement ecology on adult *T. eques* at BPFH. The first found snakes used pond edges, cattail-dominated fallow ponds, and nearby rocky, shaded slopes during the active season from March to October with home range from 0.7 ha to 4.2 ha (Boyarski et al. 2015). In addition, they did not find any evidence of territoriality in *T. eques*. The second study found both sexes used similar macro- and microhabitats, but females moved less frequently and remained near water with sparse vegetation during gestation. Both sexes made movement forays between active season habitat and over-wintering habitats prior to overwintering (Sprague and Bateman 2018). While contributing to the growing literature on *T. eques* movement ecology (e.g. Nowak et al. 2016; Emmons and Nowak 2016) and snake management at BPFH, there has yet to be a detailed study on the population ecology of *T. eques*.

Herein we present the results of a five-year mark-recapture study on *T. eques* at BPFH to assess local population dynamics, life-history, ecology, and use of hatchery ponds. We set out to measure the following: 1) temporal patterns of detection and catch per unit effort (CPUE), 2) detection and CPUE among hatchery pond substrates, 3) population structure, 4) body size and growth rates, 5) seasonal body condition index trends, and 6) snake injury rates and interactions with non-native bullfrogs. The monthly detection and CPUE information can be applied to future BPFH surveys and other *T. eques* populations to plan surveys to maximize snake detection. Inter-annual detection, demographic, and population changes will provide a comparative baseline to measure and monitor population trends at BPFH, and for other *T. eques* populations until more data are available. Individual growth rates will be useful to measure population turnover and recruitment, whereas body condition can be used as a metric to measure reproductive patterns and to detect sudden shifts in body condition that may indicate the emergence of potential stressors. The importance of the BPFH *T. eques* population cannot be overstated, and the results of this study can aid hatchery operations as well as contribute valuable information to the species management and recovery elsewhere in its distribution. This includes developing an effective and cost-efficient monitoring strategy for gartersnakes, particularly for the hatchery population to assure *T. eques* will continue to persist at BPFH.

METHODS

STUDY SITE

The 55 ha BPFH consists of the 21 ha Bubbling Ponds (BP) and 34 ha Page Spring (PS) fish hatchery properties (E 0418091 N 3847618 UTM, NAD83, 1052 m), located eight km north of Cornville, Arizona, and separated by Oak Creek (Fig. 1). There are 17 ponds at BP and two at PS (the latter is the largest trout growing facility in Arizona). The 17 ponds at BP are divided into three categories based on substrate type: 1) lined ponds with a wildlife safe rubber Ethylene Propylene Diene Monomer lining (n = 5), 2) unlined ponds (n = 7), and 3) fallow ponds (n = 4) which were no longer used for fish production and are now partially flooded and dominated by dense stands of *Typha* spp. (cattails) and willow saplings (*Salix* sp.) that are maintained for snake habitat. Both PS ponds were unlined; Show Pond offers hatchery visitors an opportunity to view large rainbow trout and provides habitat for *T. eques*, and Old Pond was drained and allowed to dry in 2009 to eliminate nonnative mosquitofish and restocked with native Gila topminnow

(*Poeciliopsis occidentalis*). Water is piped from Bubbling Springs north of BP, and temperatures in these ponds are maintained at a near constant 20°C throughout the year. Fish species produced during the course of this study included native Roundtail Chub (*Gila robusta*), Colorado Pikeminnow (*Ptychocheilus lucius*), and Razorback Sucker (*Xyrauchen texanus*), and nonnative Largemouth Bass (*Micropterus salmoides*), Redear Sunfish (*Lepomis microlophus*), and Bluegill (*Lepomis macrochirus*) (S. Gurtin, personal communication).

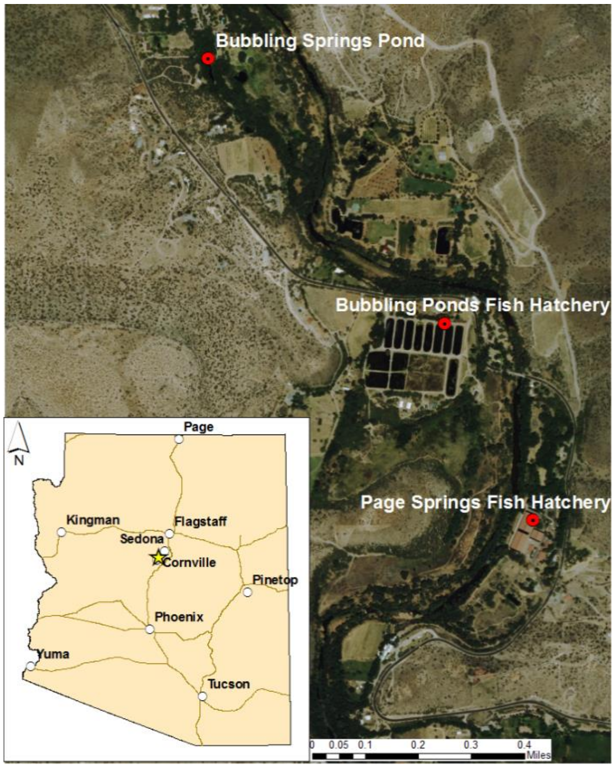


Figure 1. Location of the Bubbling Ponds Fish Hatchery Complex.

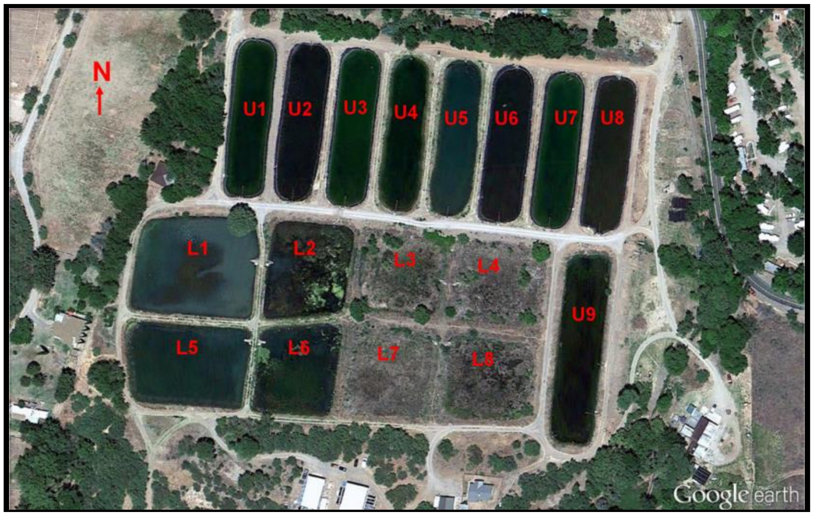


Figure 2. Aerial view of Bubbling Ponds, the primary study site, U = upper ponds, L = lower ponds.

Figure 3. Aerial view of Page Springs Show and Old ponds.

Figure 4. Approximate trap locations at BPFH and the outflow ditch.

FIELD METHODS

We collected capture-recapture data for *T. eques* at BP from 2007–2011 from seven unlined and four fallow ponds at BP (Fig 2), Show Pond and Old Pond at PS, and a short section of Oak Creek (Fig 3; Table 1). We used two passive methods to capture snakes, 0.63 cm (¼") mesh Gee® minnow traps and cover boards, and also recorded incidental/opportunistic observations. All sampling occurred from May–September, during the snake's primary seasonal active period.

Table 1. BPFH pond characteristics and annual trap effort. TD = trap days

Pond Name	Substrate	Area (m^2)	Perimeter (m)*	2007 TD	2008 TD	2009 TD	2010 TD	2011 TD
BP - U4	Unlined	2,098	216.1	78	186	132	136	128
BP - U5	Unlined	2,098	216.1	78	186	132	136	128
BP - U9	Unlined	2,669	261.5	265	310	220	200	160
BP - L1	Unlined	3,996	251.0	115	248	176	184	128
BP - L2	Unlined	2,260	189.0	214	248	176	176	128
BP - L3	Fallow	1,874	173.3	0	183	176	16	64
BP - L4	Fallow	2,104	183.8	0	117	7	16	8
BP - L5	Unlined	3,105	225.8	115	248	176	168	128
BP - L6	Unlined	2,043	181.5	28	0	0	0	80
BP - L7	Fallow	1,984	178.9	0	31	30	32	0
BP - L8	Fallow	1,961	177.3	253	279	176	128	128
Show Pond	Unlined			185	300	200	180	160
Old Pond	Unlined			122	203	112	160	112
Oak Creek	Unlined			209	248	216	160	88
Total				**1662**	**2787**	**1929**	**1692**	**1440**

Trapping: We used a robust sampling design with primary weekly sampling sessions with secondary monthly sampling sessions 3-4 times annually (Pollock et al. 1990; Mazerolle et al. 2007) at ponds and a small section of Oak Creek between BP and PS. We deployed between 50–107 Gee® minnow traps per trap period with 4–12 traps deployed at each pond from May–September during the active season. We placed traps 10–25 m apart (Fig 4), and positioned so the 2.5 cm (1") funnel entrance was situated at or slightly below water level, and secured the traps with rope to the banks. Exact trap placement varied by a few meters among trap sessions because we could not establish permanent stakes due to grounds maintenance activities. We checked traps 1–3 times/day (morning: 0730–1000 h; afternoon: 1300–1500 h; evening: 1630–1930 h) to ensure snakes were not in traps for more than 5 hours during the day. Traps were allowed to "self-bait" by accumulating small fish and tadpoles.

Cover boards: In 2007 we haphazardly placed 32 plywood cover boards, 10 long (61 x 122 cm) and 22 short (61 x 61 cm) around the BP ponds, and 2 short (61 x 61 cm) around Old Pond at PS. Cover boards were checked in the morning and evening during trapping sessions. At the end of 2007, seven short and three long boards were removed, and the remaining boards were surveyed through September 2008. Only two snakes were captured with this method, and because of the short duration of their use we do not present any further discussion on cover boards. See Appendix for further discussion on cover boards for snake detection.

Incidental observations: We, or hatchery personnel, incidentally captured snakes by hand at or near ponds while checking traps and cover boards or during daily hatchery operations. We included these captures in demographic, growth rate, and body condition analyses but not in detection and catch-per-unit-effort analyses.

SNAKE DATA COLLECTION AND MARKING

We recorded the following data for each captured *T. eques*: date, time of capture, capture status (new or marked), mark or PIT tag number, sex, weight (g), snout-vent-length (SVL mm), tail length (TL mm), age class (neonates [umbilical scar present, or born while being processed], juvenile, adult), reproductive status (gravid, non-gravid), and capture mode (trap, cover board, incidental). We noted missing or damaged tails or body scarring and scored snakes + for tail damage/missing and – for complete tails.

To ensure that individual marks were not lost over time, snakes received two marks. First, each snake received a unique ventral scale clip or scale brand with a high temperature medical cautery unit (Brown and Parker 1976; Winne et al. 2006). We branded 1–3 ventral scales anterior to the anal scale (e.g. 1–10, 20, 30…), forming a unique coding system (Winne et al. 2006). Next, we subdermally injected Biomark passive integrated transponder (PIT) tags approximately 60–90 mm anterior to the vent. Neonates and young of the year were too small for PIT tags and only received a unique ventral scale clip or brand. We released all snakes at the site of capture, except for five snakes in 2007 that were removed to be part of a pilot captive breeding program implemented by the Gartersnake Conservation Working Group at Mesa Community College (those snakes were later transferred to another permitted facility in the private sector).

ANALYSIS

Relative detection: We calculated naïve relative detection from the trap data using generalized logistic regression models. We used a binomial score of 0 = snake absent and 1 = snake present for each trap time period to estimate relative detection. This is a simplified approach comparable to more robust algorithm-based detection probability estimation approaches such as Program PRESENCE (MacKenzie et al. 2018) but is useful to track detection changes over time (Kéry et al. 2009; Ryan et al. 2014; Voyles et al. 2018). We fit the presence/absence scores to a binomial distribution with a logit function for different time periods (daily, week-long trap session [also equals month], and year), AM/PM trap checks, and pond substrate (unlined versus fallow ponds). We limited our detection analyses to the four fallow ponds and seven unlined BP ponds because those ponds had the most robust data set in terms of effort (70%) and snake captures (94%).

The statistical approach we used to estimate relative detection from presence/absence data can produce biased results from false absences, i.e., species is present at a site but goes undetected, and can underestimate parameter estimates across space and time (Gu and Swihart 2004; Kéry et al. 2009). False absences are problematic for rare species, rapid surveys with limited effort, or sampling multiple sites, all of which can increase likelihood of false absences (Banks-Leite et al. 2014). However, our study avoided these potential sources of bias because: 1) we sampled a single site, 2) snakes are known to occupy the site and were always detected during a trap period, 3) we used proven trapping techniques to enhance detection during trapping, 4) sampling sessions were >4 days and repeated multiple times per year, and 5) we treated the site as a single patch (grouping all traps/ponds together) with no partitioning of trap effort among ponds or habitats.

Relative abundance: We used raw counts and catch-per-unit-effort (CPUE) from the trap effort as a measure of relative snake abundance metrics. We tested if relative abundance varied annually or monthly, and by pond substrate (unlined versus fallow). We used generalized regression with a zero-inflated Poisson distribution to determine differences in raw counts, and CPUE varied among the aforementioned variables. Next, we transformed the raw count data per trap into CPUE by dividing the number of snakes caught by total traps x 100 (McCafery and Eby 2016). Our data set is dominated by zero observations per trap session, i.e., most traps were unoccupied when checked, and the zero-inflation Poisson penalizes and compensates for overdispersion when zeros are a large part of the data set (Crawley 2013). For both raw counts and CPUE analyses, we pooled data among years and ran individual models for each variable.

Body condition index: Body condition is a variable phenotypic trait that refers to the available energy reserves of an animal for daily and life time activities (Green 2001; Labocha et al. 2013). Ecologists use body condition indices to quantify energy reserves and how they can affect movement ecology (Lowe et al. 2006), mortality (Shine et al. 2000), reproductive phenology and output (Bonnet and Naulleau 1996), and individual and population responses to threat stressors (Stevenson and Woods 2006; Reading 2007; Waye and Mason 2008). We used the scaled mass index (SMI) to calculate snake body condition as an assay of energy stores or animal health (Bradshaw et al. 2000; Green 2001). SMI accounts for scaling relationships between measures of body size and mass that may be sensitive to individual or population level variation (Peig and Green 2009). We used mass and SVL measurements for all captured snakes. For snakes recaptured within a single sampling period, we used the first set of mass and SVL measurements; for snakes captured among sampling periods but within the same year, we used the mean mass and SVL for SMI calculations. We calculated SMI as

$$M_i = M * (SVL_0/SVL)^{b_{SMA}}$$

where M is mass (g), SVL (snout-vent-length, mm) of the individual snake, SVL_0 is the arithmetic mean of the population SVL, and b_{SMA} is the standardized slope from the ln(mass) versus ln(SVL) regression of the population (Peig and Green 2009; Peig and Green 2010). Because age classes, i.e., neonates, juvenile, and adults, differ in body size, and *T. eques* exhibits sexual size dimorphism (Valencia-Flores et al. 2018), we calculated SMI by age class and sex separately. We used Rosen and Schwalbe's (1988) estimated adult size at sexual maturity (500 mm SVL for males and 550 mm for females) to assign age class designations. We calculated SMI for each age class: neonates = <185 mm SVL, young of year (YOY) 220–299 mm SVL, and juveniles = 300–500 mm SVL for males and 300–550 mm SVL for females. Because SMI may be affected by whether or not a snake has recently eaten we excluded snakes with an obvious prey bolus, as well as for gravid females, which give birth in May or early June (Sprague and Bateman 2018).

We used generalized linear models to test if SMI differed between adult and juvenile sexes, monthly, and annually. We then compared SMI for all snakes with and without injuries, i.e. scarring or missing tails, by pooling all captures among years.

Growth rates, body size, & population structure: Body size distribution is an important demographic trait that can be used to monitor populations, especially for species of conservation concern (Willson et al. 2006; Kim et al. 2018). Combining both trap and incidental captures, we used SVL to describe body size structure, instead of total length because of missing or damaged tails. For snakes captured more than once per year, we used the mean SVL of all captures, and for snakes caught in multiple years, we used the most recent SVL measurement for analyses. We binned 188 snakes into 12 discreet 50 mm SVL categories and used ordinal logistic regression to test if size class structure varied among years. We excluded neonates from the body size distribution analyses because they were born from females being held for processing and are not representative of the number of neonates in the general population. We used ANOVA to compare SVL between adult and juvenile females and males. We used logistic regression to compare differences in SVL, tail length (excluded snakes with tail damage), and SVL-tail length ratio between adult male and female snakes. We used least squares regression to test if tail length differed among age classes by sex.

We calculated growth rate as the change (Δ) in SVL between two capture occasions divided by the number of days between captures (ΔSVL/Δdays) (Coates et al. 2009). Using daily growth rates, we then calculated annual growth rate scaled for 245 active growing days per year at BPFH. The estimated growth season for *T. eques* is 245 days, between 1 March and 31 October at BPFH (Boyarski et al. 2015; Sprague and Bateman 2018), and calculating total growth days between recaptures provides a more accurate assay of growth rates than using total annual days (Bronikowski and Arnold 1999). We used ANOVA to compare intersexual growth rates among adults, juveniles, and neonates and then used linear regression to determine if growth rates changed in relation to SVL for males and females.

Sex ratio is an important demographic trait critical in understanding population dynamics, and sex biased captures can bias demographic population trend estimates (Lee et al. 2011). We calculated annual operational sex ratio as the ratio of adult and juvenile males to females captured, and we excluded 14 snakes because their sex was not determined at time of capture. We used χ^2 to test whether sex ratio varied by year and month for trapped animals.

RESULTS

Relative detection and relative abundance: We captured a total of 237 *T. eques* and marked 188 individuals in 9,510 trap days, over 16 sampling sessions (i.e., consecutive day surveys) from 2007–2011 (Table 2). We captured 154 individuals at Bubbling Ponds (BP), 23 at Page Springs (PS), and two in Oak Creek. Since BP had the largest number of captures, 81% of individuals and 72% of captures, we only present detection analyses for site and not the others due to too few data.

Number of traps per survey ranged from 17–107 and snake detection per sampling period was not affected by the number of traps set ($P = 0.8785$, $\chi^2_{1,122} = 0.023$) (Fig 5). Relative detection differed by year and AM/PM trap check, but not by month or pond substrate (Table 3). Mean annual relative detection was greatest at BP compared to the other sites (Fig 6) and mean monthly relative detection at BP was lowest in May but consistently high from June to September (Fig 7). Raw snake counts and catch-per-unit-effort (CPUE) at BP varied by year (Fig 8), month (Fig 9), and AM/PM trap check, and there was no difference by pond substrate type (Table 4). Because of small sample sizes at PS and Oak Creek we could not conduct similar analyses.

Table 2. Annual and monthly trapping effort summary for the BPFH Complex, including BPFH, Old Pond (PSOP), Show Pond (PSSP), and Oak Creek. TD = trap days

Year Month	# Traps Set	Total TD	BPFH TD	PSSP TD	PSOP TD	Oak Creek TD	Sampling Dates
2007							
June	50	350	259	42	28	21	19–22 Jun
July	50	345	266	35	30	14	17–20 Jul
August	50	442	306	54	28	54	14–17 Aug
September	55	525	315	54	36	120	10–14 Sep
2007 Total		**1662**	**1146**	**185**	**122**	**209**	
2008							
May	85	595	420	70	49	56	13–16 May
June	85	595	420	70	49	56	24–27 Jun
July	85	741	540	80	49	72	21–25 Jul
August	107	856	656	80	56	64	18–22 Aug
2008 Total		**2787**	**2036**	**300**	**203**	**248**	
2009							
May	90	630	434	70	56	70	12–15 May
Jun	95	742	512	70	56	104	15–19 Jun
Jul	81	557	455	60	0	42	14–17 Jul
2009 Total		**1929**	**1401**	**200**	**112**	**216**	
2010							
June	86	688	464	80	64	80	14–18 Jun
July	86	688	464	80	64	80	12–16 Jul
August	84	316	262	20	32	0	9–11 Aug
2010 Total		**1692**	**1190**	**180**	**160**	**160**	
2011							
June	90	720	544	80	48	48	20–24 Jun
August	90	720	536	80	64	40	22–26 Aug
2011 Total		**1440**	**1080**	**160**	**112**	**88**	

Table 3. Generalized logistic regression (GLM) comparing relative trap detection by year, month, AM/PM trap check, pond substrate, and site. *Denotes significance.

Model	*P*	χ^2	DF	Relative Detection
Year	0.0412*	9.95	4	0.94 (0.67–0.99)
Month	0.1182	7.35	4	0.62 (0.28–0.87)
AM/PM	0.0367*	4.36	1	0.25 (0.18–0.34)
Pond Substrate	0.5784	0.30	1	0.97 (0.97–0.98)

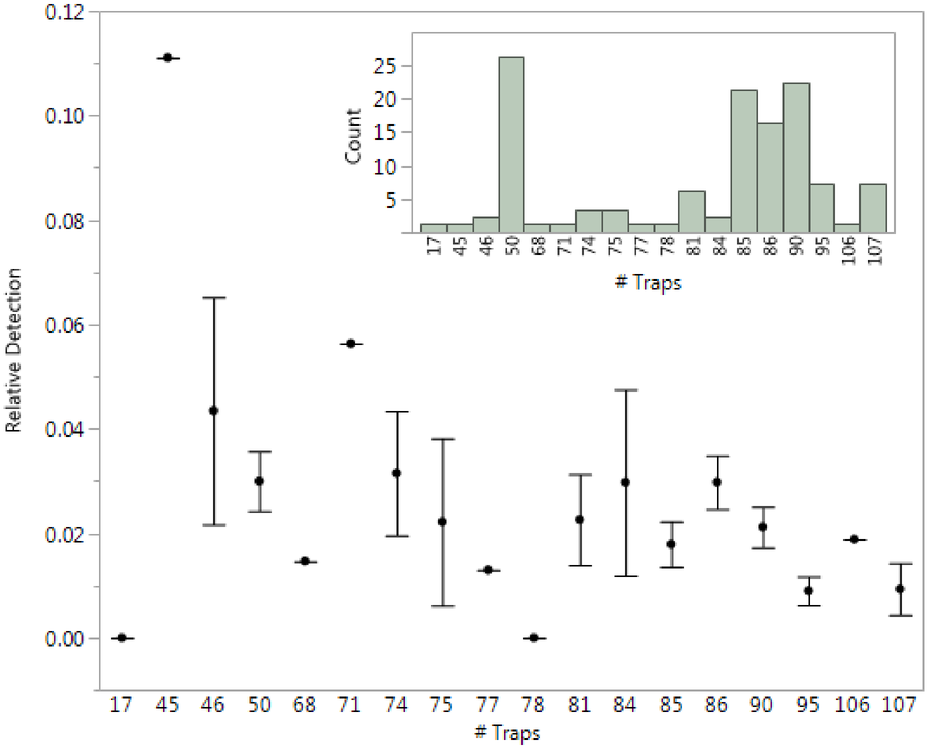


Figure 5. Mean (SE) relative detection by number of traps per sampling period. Inset is number of surveys by number of traps.

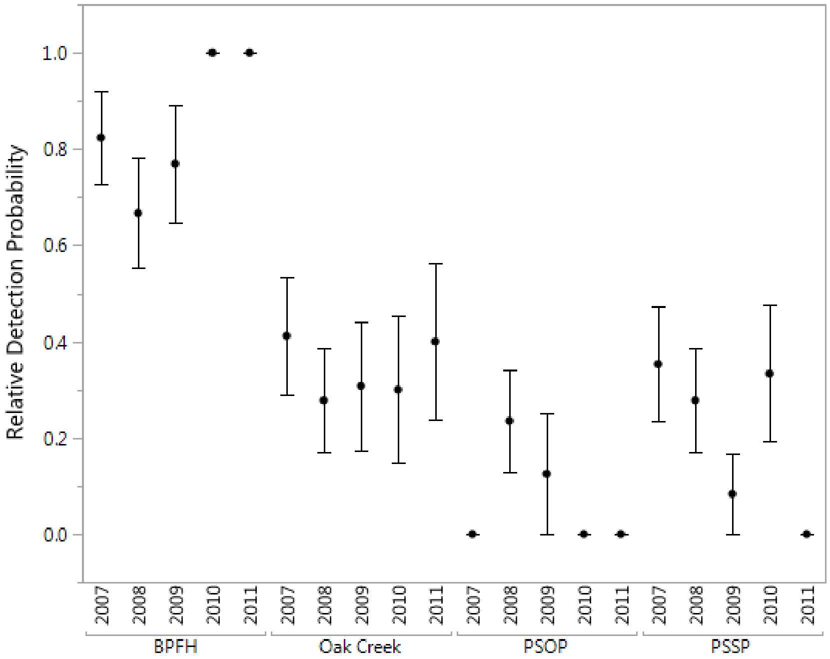


Figure 6. Mean (SE) annual relative detection for the 11 ponds at Bubbling Ponds (BPFH), Oak Creek, Old Pond (PSOP), and Show Pond (PSSP).

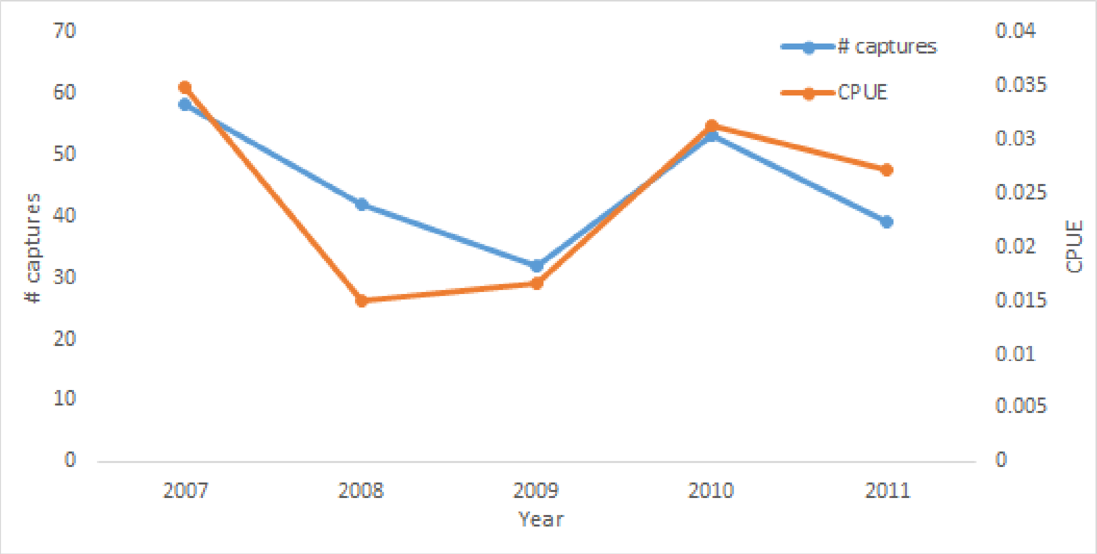


Figure 7. Annual variation in raw T. eques *captures and catch-per-unit-effort (CPUE).*

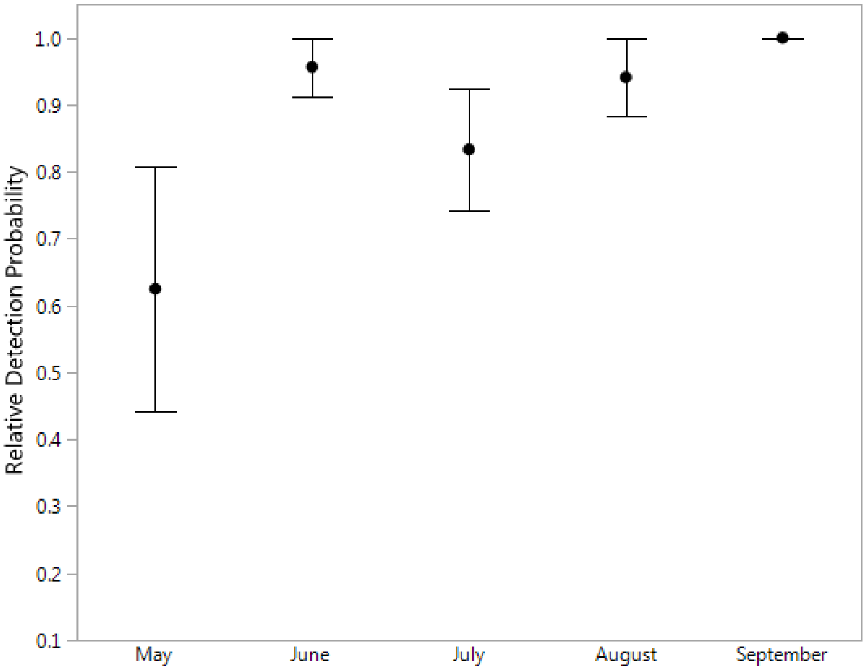


Figure 8. Mean (SE) monthly relative detection for all study ponds and years (2007–2011).

Table 4. Generalized logistic regression results for capture and catch-per-unit-effort (CPUE) counts by year, month, AM/PM trap check and pond substrate. *Denotes significance.

Model	*P*	χ^2	DF		Model	*P*	χ^2	DF
Count					**CPUE**			
Year	0.0001*	23.93	4		Year	0.0001*	41.61	4
Month	0.0137*	12.55	4		Month	0.0066*	14.22	4
AM/PM	0.0001*	40.21	1		AM/PM	0.0001*	24.03	1
Pond Substrate	0.3858	0.75	1		Pond Substrate	0.2712	1.21	1

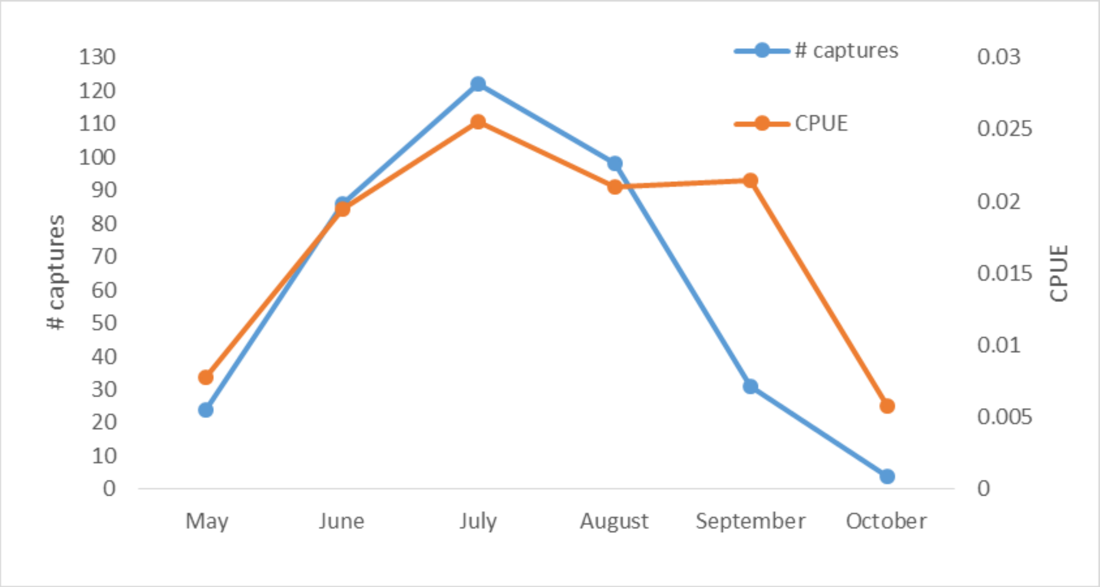


Figure 9. Monthly (all years combined) variation in T. eques captures and catch-per-unit-effort (CPUE).

Population characteristics: We observed an SVL range from 106–946 mm for all captured snakes and for those born to females held temporarily (Table 5). SVL body size structure of snakes > 300 mm SVL differed among years (*P* = 0.0064, $\chi^2_{4,188}$ = 14.28; Fig 10), as did size class kernel smoothing (*P* = 0.0086, $\chi^2_{4,188}$ = 13.62; Fig 11). On average, adult females were 21% larger than males (*P* = 0.0001, $F_{1,100}$ = 52.55), but juvenile SVL did not differ by sex (*P* = 0.9571, $F_{1,62}$ = 0.0029). Tail length not scaled for SVL did not vary by gender between adults (*P* = 0.1793, $F_{1,79}$ = 1.83), juveniles (*P* = 0.1245, $F_{1,48}$ = 2.18), YOY (*P* = 0.1345, $\chi^2_{1,12}$ = 2.52), or neonates (*P* = 0.6425, $\chi^2_{1,66}$ = 0.44), but tail length scaled for SVL was significantly greater in adult (*P* = 0.0001, $F_{1,79}$ = 116.59,) and juvenile (*P* = 0.0001, $F_{1,48}$ = 25.94) males over females (Fig 12).

Table 5. Mean (± StDev) SVL, tail, total lengths (mm), and mass (g) (range and sample size in parentheses). We excluded snakes with damaged tails for tail length, total length, and tail/SVL ratio calculations. Neonate lengths taken at birth.

Sex/Age	SVL	Tail Length	Total Length	Mass	Tail/SVL
♀ (adults)	747.3 ± 116.5 (550–946, 73)	197.9 ± 35.7 (85–260, 58)	934.9 ± 135.5 (714–1196, 58)	175.7 ± 83.8 (56–448, 70)	0.27 ± 0.04 (0.12–0.32, 58)
♂ (adults)	592 ± 61.3 (501–714, 39)	183.4 ± 35.3 (77–233, 27)	780.6 ± 87.4 (614–938, 27)	88.0 ± 28.4 (41–149,38)	0.30 ± 0.05 (0.14–0.34, 27)
Juveniles	406.3 ± 69.6 (300–546, 69)	124.8 ± 25.2 (72–170, 67)	531.3 ± 91.3 (394–700, 67)	29.7 ± 13.9 (11–68, 69)	0.30 ± 0.03 (0.15–0.37, 67)
YoY	261.8 ± 18.5 (227–296, 23)	79.8 ± 9.5 (64–95, 23)	341.6 ± 24.3 (300–381, 23)	9.8 ± 2.6 (5–15, 23)	0.30 ± 0.03 (0.26–0.36, 23)
Neonates	183.1 ± 13.7 (106–216, 85)	55.7 ± 7.8 (19–69, 85)	238.8 ± 17.5 (155–278, 85)	3.3 ± 0.6 (1–5, 85)	0.30 ± 0.04 (0.10–0.46, 85)

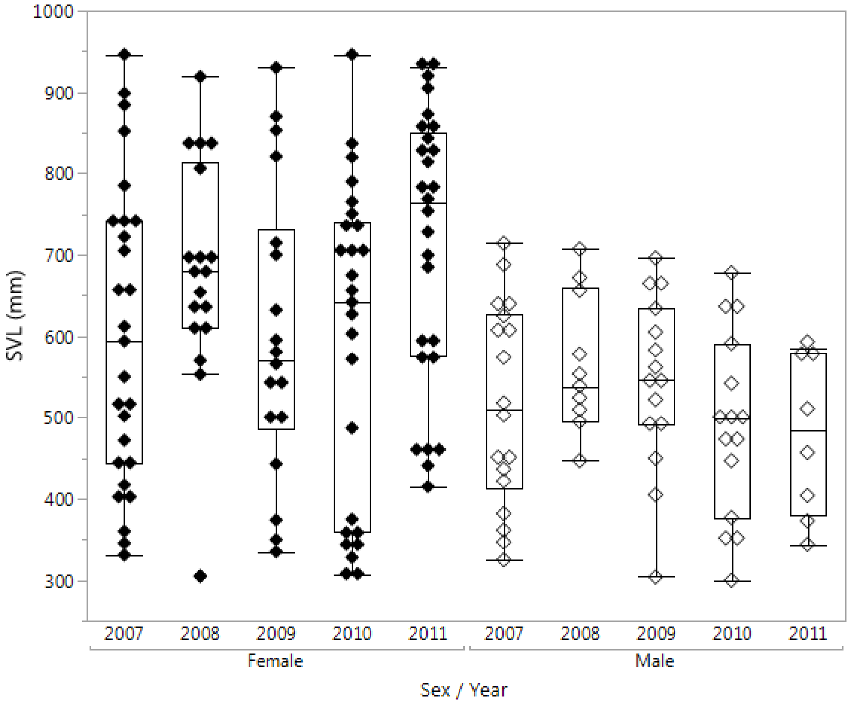


Figure 10. Mean annual SVL (mm) of all captured adult and juvenile snakes by sex (females n = 116, males n = 66) from BPFH complex.

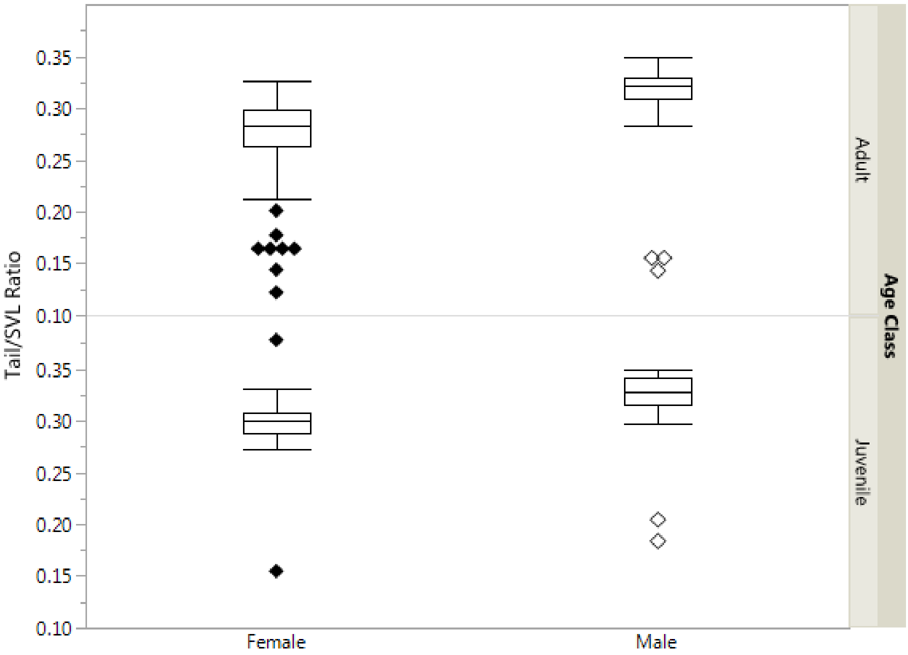
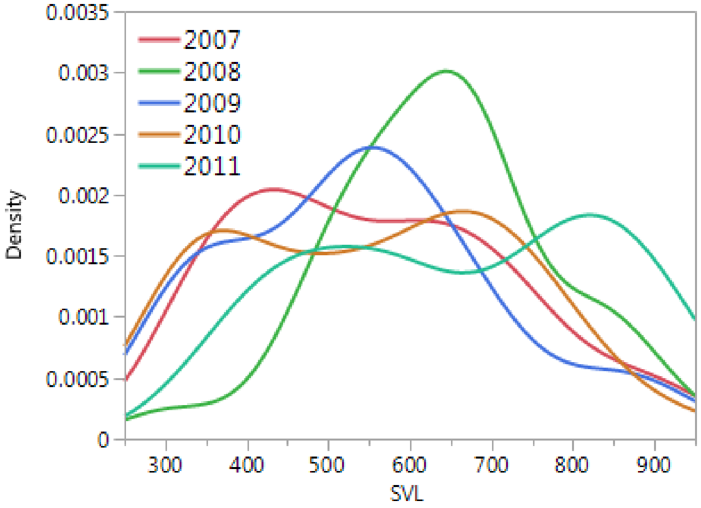
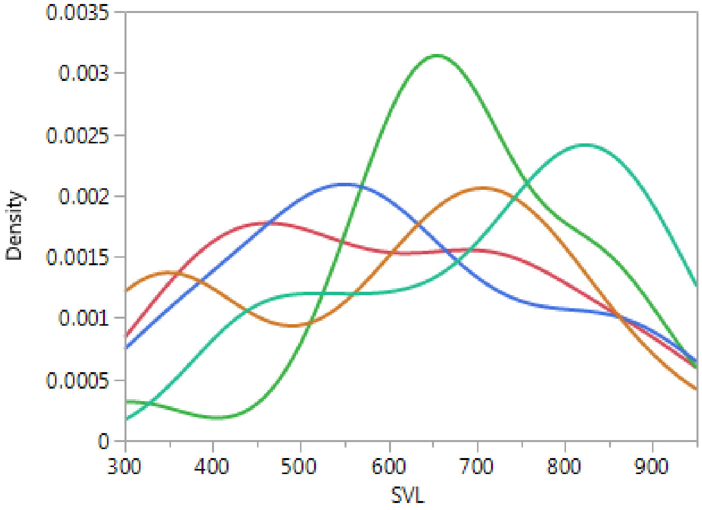


Figure 11. Annual SVL/tail ratio (SE) by sex and age class.

A. All snakes (juveniles and adults)



B. Females



C. Males

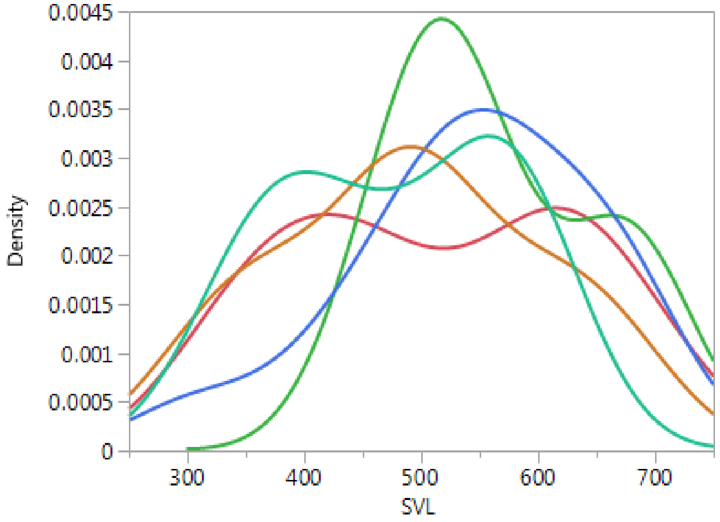


Figure 12. Annual SVL size distribution with density kernel smoothing curve.

Male neonate growth rates ($P = 0.005$, $F_{1,26} = 38.28$) were significantly faster than females, but there was no gender difference in growth rates of juveniles ($P = 0.0753$, $F_{1,7} = 5.01$) or adults ($P = 0.0949$, $F_{1,42} = 2.91$; Table 6; Fig 13). Growth rate decreased with size for both females ($P = 0.0001$, $r^2 = 0.84$) and males ($P = 0.0001$, $r^2 = 0.75$), and linear growth rate change was slower in females (slope, 211.6–0.2 SVL) than males (slope, 286.5–0.3 SVL) (Fig 14).

Table 6. Mean annual growth rates (mm ± SE) and ANOVA results of age class growth rates between sexes. *Denotes significance. Sample size in parentheses.

Age class	♀	♂	*P*	F-ratio
Adults	52.1 ± 5.2 (26)	61.6 ± 7.6 (11)	0.9435	0.005
Juveniles	85.6 ± 10.2 (7)	102.5 ± 14.6 (3)	0.2036	2.30
Neonates	153.1 ± 13.5 (4)	173.1 ± 11.3 (5)	0.0005*	38.21
All Stages	69.3 ± 7.6 (37)	97.4 ± 10.6 (19)	0.0026*	9.90

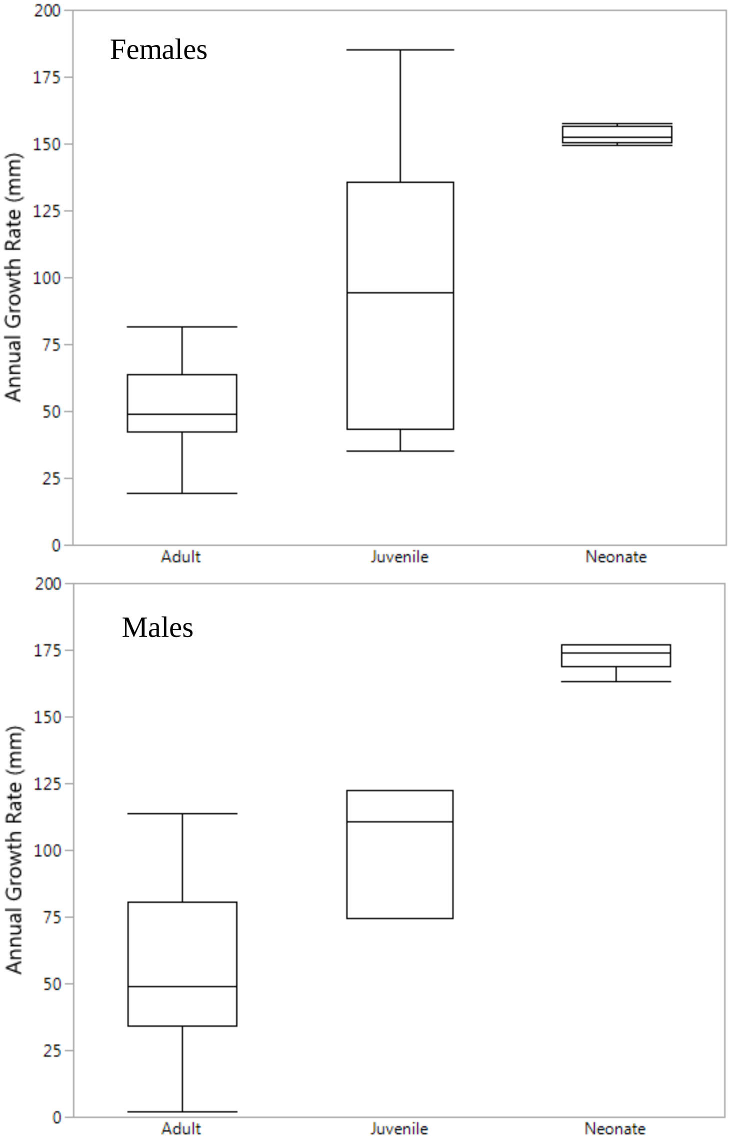


Figure 13. Mean (SE) annual growth rate by age class for females and males.

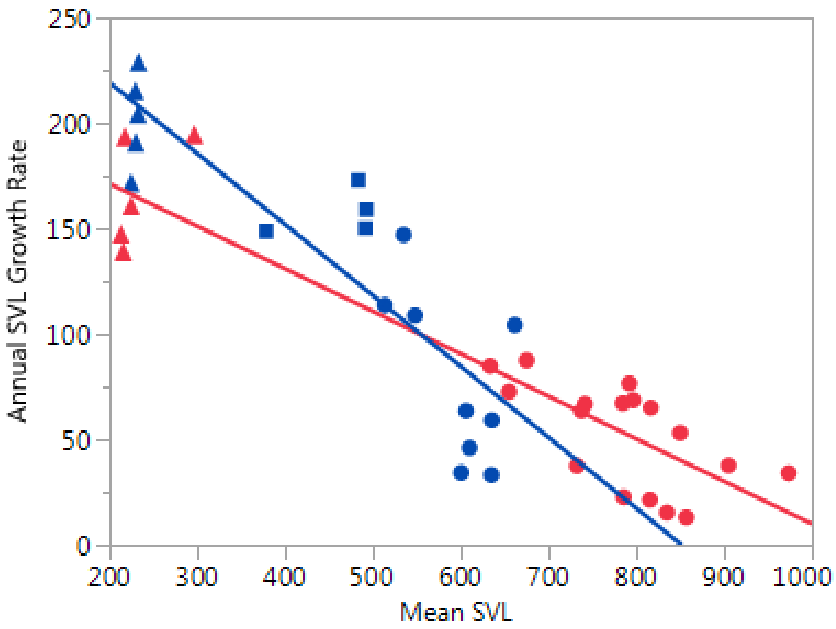


Figure 14. Linear regression relationship of mean SVL and annual growth rate. Red line and symbols = females, blue line and symbols = males; ▲ = neonates, ■ = juveniles squares, ● = adults.

The overall adult and juvenile sex ratio for all years and captures (traps and incidental observations) combined was 1.7:1 F:M, but was significantly female biased, 2.4:1 F:M, from trap captures, and was female biased during most years (Table 7). Monthly trap capture sex ratio was significantly females biased in June and July and roughly equal in May, August and September (Table 8), and females biased in unlined ponds (1.7:1 F:M, $P = 0.0023$, $\chi^2 = 9.32$) and fallow ponds (2.71:1 F:M, $P = 0.0052$, $\chi^2 = 7.81$).

Table 7. Annual adult and juvenile sex ratios for incidental and trapped *T. eques*, χ^2 results are for trap captures. Incidental captures were too small low for analysis. Count totals summed for individual years differ from the sum of 2007–2011 because we excluded recaptured individuals for the 2007–2011 sex ratio calculation. *Denotes significance.

Year/Method	F:M Ratio	# ♀	# ♂	χ^2	*P*
Incidental					
2007–2011	2:1	12	6		
Trap					
2007	1.7:1	30	17	3.59	0.0579
2008	1.9:1	22	11	3.66	0.0555
2009	2.4:1	22	11	3.66	0.0555
2010	1.75:1	25	14	3.10	0.0782
2011	3.3:1	27	8	10.31	0.0013*
2007–2011	2.4:1	126	61	22.59	0.0001*
Incidental and Trap					
2007–2011	1.7:1	113	59	16.95	0.0001*

Table 8. Monthly adult and juvenile trap capture sex ratios and χ^2 results. *Denotes significant.

Month	Sex Ratio	# ♀	# ♂	χ^2	P
May	0.7:1	6	9	0.60	0.4370
June	2.7:1	41	15	12.07	0.0005*
July	3.0:1	43	14	14.75	0.0001*
August	1.6:1	36	22	3.37	0.0660
September	1.4:1	7	5	0.33	0.5637

Body condition index and tail injuries: Both mass-length and scaled mass index (SMI) had the same significant relationship for males ($P = 0.0001$, $F_{1,26} = 10323.6$, $r^2 = 0.99$) and females ($P = 0.0001$, $F_{1,90} = 5335.6$, $r^2 = 0.98$). Therefore, we used SMI for all further body condition index analyses. Adult female SMI was greater than males (Whole Model: $P = 0.0001$, L-R, $\chi^2_{2,106} = 768.0$; Sex $P = 0.0001$, SVL $P = 0.6113$), and there was no difference between female and male juveniles (Whole Model:, $P = 0.9029$; Sex $P = 0.9546$; SVL $P = 0.6553$, L-R $\chi^2_{2,48} = 0.20$). There was a positive effect of month on adult female SMI ($P = 0.0001$, $F_{1,38} = 34.56$) and no effect on male ($P = 0.3436$, $F_{1,26} = 4.49$) or all juvenile snakes ($P = 0.9772$, $F_{1,38} = 1.19$) (Table 9; Fig 15). Tail injuries occurred in 20.1% of *T. eques* and SMI of snakes with missing or scarred tails did not differ from non-injured adults ($P = 0.0945$, $F_{1,109} = 2.79$,) or juveniles ($P = 0.7163$, $F_{1,52} = 0.13$). (Fig 16).

Table 9. Monthly (all years combined) mean (±StDev) SMI (body condition). Range in parenthesis.

	May	June	July	August
♀ (adult)	167.5 ± 23.2 (151.0–183.9) $n = 2$	150.7 ± 24.8 (104.6–207.4) $n = 33$	168.3 ± 17.9 (140.9–202.0) $n = 21$	189.0 ± 17.9 (161.9–215.2) $n = 11$
♂ (adult)	82.6 ± 12.5 (70.5–102.1) $n = 6$	82.9 ± 9.9 (68.5–100.7) $n = 11$	88.5 ± 7.1 (76.4–95.5) $n = 9$	87.2 ± 7.8 (76.9–97.2) $n = 8$
Juveniles	24.7 ± 4.3 (20.1–29.8) $n = 4$	27.9 ± 2.8 (23.0–32.3) $n = 9$	30.4 ± 4.4 (24.7–37.8) $n = 15$	26.2 ± 4.8 (18.6–35.1) $n = 23$
YOY	NA	9.1 ± 1.7 (7.9–10.4) $n = 2$	10.1 ± 1.7 (7.8–12.1) $n = 10$	NA
Neonates	NA	3.4 ± 0.3 (2.5–4.0) $n = 69$	NA	NA

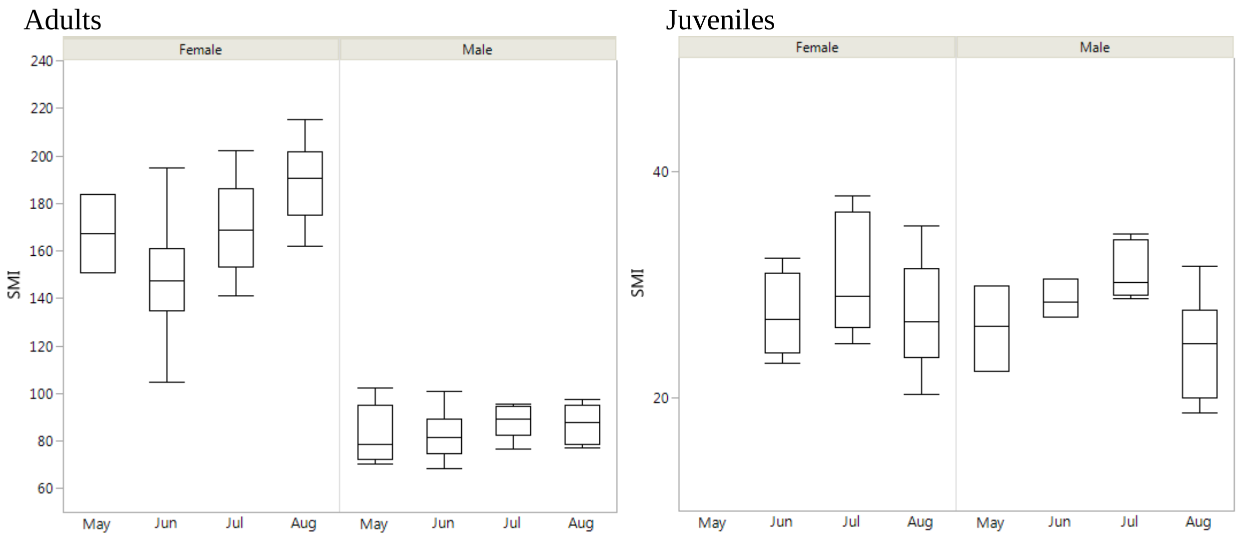


Figure 15. Mean (SE) monthly SMI for adult and juvenile snakes by sex.

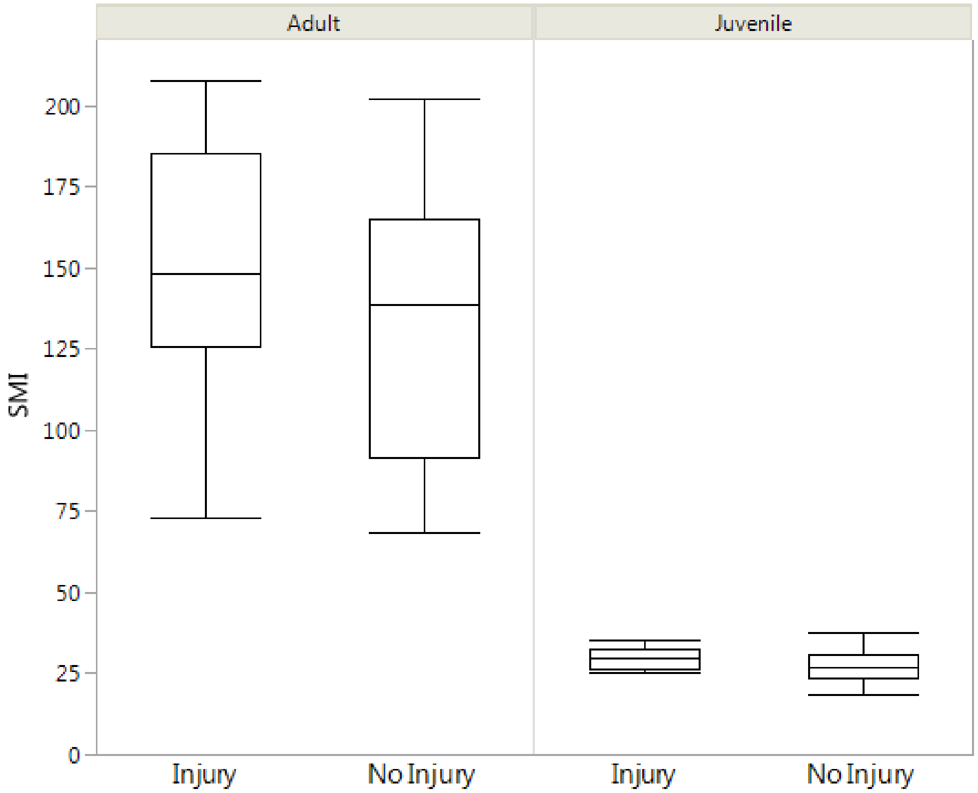


Figure 16. Mean (SE) SMI of adult and juvenile snakes with and with tail injuries.

DISCUSSION

The Bubbling Ponds *T. eques* population occupies a unique landscape that is heavily managed and modified with a large number of potential threats, including the presence of nonnative bullfrogs, predatory fishes, wading birds, and raptors, and a light- to moderately traveled dirt-road system within and adjacent to the hatchery. Despite these threats, this *T. eques* population is considered one of the largest populations in the United States (USFWS 2014). Because of the ease of site access and species detection, this population is a model system to test field techniques, assess threat risk, estimate life history parameters, measure population dynamics, and study other aspects of the species' ecology that can provide inferences to management, recovery, and monitoring of more natural populations.

The annual relative abundance and detection of *T. eques* at BP was consistent and supported a diverse suite of age classes from 2007–2011. While easy to detect at BP, *T. eques* is difficult to detect elsewhere in Arizona due to a combination of rarity, habitat complexity, and secretive habits (Rosen and Schwalbe 1988; Rosen et al. 2001; Holycross et al. 2006; Emmons 2017; Jones et al. in press). We captured snakes so frequently that we had perfect detection during each multi-day trap session, but this is not the case at most other known populations (Rosen and Schwalbe 1988; Holycross et al. 2006). At this time it is not possible to compare relative abundance and detection rates to other *T. eques* trap studies because many of those raw data are not available for comparative analyses, but such a comparison should be a priority.

Detection and Sampling Methods

Our study design with 4–5 day trap sampling periods was very effective in detecting *T. eques* at BP and yielded perfect detection during multi-day trap periods and a 25% daily snake detection rate. Surprisingly, the number of traps per survey, ranging from 17 to 90, did not affect snake detection. Species detection is affected by abundance and sampling effort, and detection should increase with effort (e.g. Kéry et al. 2009; Durso et al. 2011), but this was not the case in our study. There are three possible explanations for this result: 1) *T. eques* at BPFH are abundant enough that our multiday sampling sessions were sufficient for snake detection independent of trap number, 2) we did not conduct enough surveys with 17–50 traps per session to allow for a more robust and balanced comparison, but this was not the goal of this study, and 3) we might observe a correlation with more robust analyses that account for imperfect detection, and this point still needs to be addressed. Regardless, the ease of detection at BP is unique compared to other *T. eques* populations (Rosen and Schwalbe 1988; Jones et al. in press) and it is not currently possible to make direct comparisons with other trap studies in Arizona.

To make the best-informed management decisions requires reliable inferences from sufficient surveys and high quality data. False-negative detections plague difficult to detect species surveys (Tyre et al. 2003), but can be accounted for with a sufficient number of repeated surveys (Thompson 2004; MacKenzie and Royle 2005). Currently, there is no minimum survey effort standard, either days or number of traps, to provide a metric of confidence of *T. eques* false-detections. One approach to resolve this issue is a survey effort occupancy study to test whether detection varies under different effort treatments, and identify a minimum number of surveys for species detection (e.g., MacKenzie and Royle 2005). BP is the ideal location for such a study because we have baseline detection rates for a comparative study.

A second approach is a meta-analysis incorporating *T. eques* historical trap efforts throughout Arizona, which vary in effort, to estimate trap detection rates under different efforts and assess overall geographic and habitat detection rate variability. Such a study will provide a justification to set a standardized minimum sampling effort that could be applied to presence/absence surveys at historic or currently occupied, or presumed extirpated, *T. eques* sites (e.g. Rosen et al. 2001; Holycross et al. 2006; Emmons 2017). But, such an analysis is hampered at this time because much of the historic raw trap effort data are not available for a meta-analysis. The lack of raw data is a hindrance to State and Federal agencies tasked with species recovery and we recommend permitting agencies require submission of raw trap data during reporting, instead of traditional effort summary tables. Such a requirement will allow for updated trend analysis as new data are collected and be available for new statistical methods as developed, allowing conservation managers to rapidly adapt needs and recovery priorities to account for changing and stochastic conditions. Most importantly, species recovery can take decades and centralized long-term archiving of invaluable survey data will prevent the accidental loss of data when researchers are no longer available.

While we had high trap success there was a strong tendency towards trapping female *T. eques* over males at BP, a pattern also seen at populations on the upper Santa Cruz River (2.3:1 F:M; AZGD, unpublished) and on the Appleton-Whittell Research Ranch (1.3:1 F:M ; d'Orgeix 2011) in southern Arizona. A biased sex ratio may represent the actual population F:M ratio, but unbalanced sex ratios are relatively rare, and when they occur may be indicative of serious demographic risks threatening a population (Ancona et al. 2017). Considering the F:M ratio among *T. eques* populations in Arizona using similar capture methods we suggest that females may be 'trap happy' and/or males are 'trap shy', but this warrants further study. Many gartersnakes exhibit roughly equal sex ratio (e.g., Lind et al. 2005; Wylie et al. 2010; Gray and Lethaby 2017), but this can be skewed by behavioral and habitat differences (Parker and Plummer 1987) and sampling technique (Wylie et al. 2010). For instance, in *T. gigas* sex ratios were 1:1 using traps, but a female-biased (1.8:1) visual encounter survey ratio because females are larger and more easily observed than males (Prior et al. 2001; Wylie et al. 2010), and adult sex ratios of *T. eques* in Mexico were 1:1.6 female biased for snakes caught by hand (Manjarrez 1998). A gender specific trap bias can be problematic in mark-recapture studies by providing imprecise detection and survival estimates (Pollock et al. 1990). Therefore we need to evaluate alternative approaches to increase male captures to improve mark-recapture analysis and parameter estimations.

Our trap present/absent treatment is a reliable method for population monitoring and our naïve relative detection and catch-per-unit-effort (CPUE) metrics are informative to measure and identify broad trends at BPFH (Kéry 2002; MacKenzie et al. 2003). But statistical techniques that estimate demographic parameters, and account for imperfect detection, can be more accurate and should be pursued in the future at BPFH and other sites (MacKenzie et al. 2018). The trade-off with our simplified approach is it can be done quickly, is flexible to discrepancies in effort, and is not as vulnerable to small sample sizes (i.e., low snake detection) that often plague snake surveys (Mazerolle et al. 2007; Durso et al. 2011). As more capture data are compiled from long-term efforts, the accuracy of the more robust analytical methods should improve, but currently most *T. eques* study sites do not meet this criterion.

Demographics & body condition

Annual *T. eques* relative detection and relative abundance (i.e., CPUE) fluctuated among years (Figs 6 and 7) similar to *T. gigas* (Halstead et al. 2015), *T. sirtalis tetrataenia* (Halstead et al. 2011), and *T. atratus* (Lind et al. 2005), suggesting this population does not exhibit dramatic short-term fluctuations in annual abundance. This inference may be improved by incorporating annual survival into detection models. It is difficult to accurately determine our observed annual fluctuations but they may be driven by climatic conditions, resource availability, or demographic processes and reproductive frequency. In more natural systems snake abundance and reproductive frequencies reflect prey availability and cycles which can be driven by rainfall or water levels (Bonnet & Naulleau 1996; Madsen and Shine 2000). Resource availability at BPFH are relatively stable since water levels and fish prey are managed and the presence of a large population of bullfrogs, which are also prey items, yet it appears the *T. eques* here fluctuate in a similar manner to populations in more natural settings.

The frequency of reproduction and the annual proportion of females that produce off-spring each year are key demographic factors that influence abundance and population growth in snakes (Miller et al. 2011), and may be responsible for the annual variation in abundance we observed. Bi- or triennial reproductive patterns in snakes can lead to abundance fluctuations during peak reproductive years (Houston and Shine 1994; Shine 2003). Rosen and Schwalbe (1988) were the first to suggest that female *T. eques* may not produce young every year, and this pattern has been observed in *T. eques* in Mexico (García and Drummond 1988; Goldberg 2004). We observed gravid females and neonates in two out of five years, 2009 and 2011, supporting a staggered reproductive strategy in *T. eques*. But, our sampling techniques may not be ideal for small neonate snakes and females are more sedentary during gestation and we cannot rule out the possibility that births and gravid females went undetected.

Thamnophis eques female body condition (SMI), was greater than males, in both SVL scaled and unscaled calculations, which was expected because SMI is influenced by length and body mass (Peig and Green 2009). Male and female SMI differed greatest in May, when females are most likely to be gravid and exhibit reduced movements during gestation (Sprague and Bateman 2018), but may this be an artifact of small sample sizes and low May trap effort, and this interpretation may be unreliable at this time. Both female and male SMI increased from June through August, likely driven by recovery from reproductive costs and overwintering (Bonnet and Naulleau 1996; Coates et al. 2009; Sivan et al. 2015).

We consistently found a diverse distribution in body size of snakes >300 mm SVL, which is consistent with a stable and healthy gartersnake population (Halstead et al. 2011). Body size distributions skewed toward smaller individuals can indicate high adult mortality, whereas skewness towards large individuals can indicate high neonate or juvenile mortality (Prival and Schroff 2012). We were unable to include neonates in our body size distribution because they were not efficiently captured with minnow traps, an inherent problem with many snake studies (Parker and Plummer 1987; Willson et al. 2008). The problem of rarely encountering small snakes, especially when it may be due to methodological techniques, can lead to potentially incorrect inferences of low neonate or juvenile survival (Parker and Plummer 1987; Willson et al. 2008). A concerted effort to detect small snakes should be a priority for conservation-oriented population monitoring to estimate demographic parameters for these important size classes. Future studies at BP and other sites should incorporate alternative methods such as cover boards, modified minnow traps, or other methods to increase detection of small snakes (Prior et al. 2001; Halstead et al. 2013; Halliday and Blouin-Demers 2015).

Thamnophis eques has the largest magnitude of female sexual size dimorphism (SSD) among *Thamnophis* (Table 10). Female-biased SSD is an important evolutionary trait in snakes (King 1989; Shine 1994; Cox et al. 2007) that is thought to have arisen to convey a reproductive advantage of large clutch size and lifetime reproductive output (Fitch 1981; Rossman et al. 1996; Manjarrez et al. 2014). Mean *T. eques* clutch size, 17.6 across Arizona, is above average for *Thamnophis* (Rosen and Schwalbe 1988; Jones et al. in review), but we lack information on female lifetime reproductive output. Alternatively, it has been hypothesized that SSD can be driven by habitat, ecological or sex-differences, specifically in prey selection where the larger sex has a larger head and ingests larger prey (Shine 1991). Camilleri and Shine (1990) showed that snake head morphology is driven by dietary divergence and not allometry. In Mexico, larger *T. eques* consumed larger prey such as fish and tadpoles, with no dietary gender difference (Manjarrez et al. 2017). A better understanding of SSD in *T. eques* can elucidate if, or how, the sexes use resources across time and space to identify critical prey items or microhabitats (Shine 1989).

Table 10. *Thamnophis* mean body size and sexual size dimorphism (SSD) comparison. Mean clutch size range from Rossman et al. (1996) and are from multiple sources, raw clutch size ranges in parentheses when data were available.

Species	Adult SVL	SSD	Mean clutch size range	Body size source
T. brachystoma	♀ 315.8 ♂ 273.4	0.15	7.2–8.8	Gray & Lethaby (2017)
T. butleri	♀ 369.0 ♂ 338.0	0.09	8.5–11.0 (6–20)	Shine (1994)
T. eques	♀ 747.3 ♂ 592.0	0.26	13.6–25.6 (9–43)	This study
T. gigas	♀ 692.0 ♂ 581.0	0.19	NA (10–46)	Halstead et al. 2015
T. hammondi	♀ 300.0 ♂ 282.0	0.06	15.6	Shine (1994)
T. marcianus	♀ 538.1 ♂ 609.8	0.08	13.2–15.3 (5–31)	Seigel et al. (2000)
T. proximus	♀ 537.0 ♂ 490.0	0.10	8.4–12.98	Shine (1994)
T. radix	♀ 584.7 ♂ 483.1	0.21	10.0–29.5 (3–36)	Stanford & King (2004)
T. radix	♀ 463.6 ♂ 407.7	0.13	9.0–11.9	King et al. (1999)
T. sauritus	♀ 483.0 ♂ 410.0	0.18	6.0–12.2 (3–26)	Shine (1994)
T. sirtalis	♀ 542.3 ♂ 450.8	0.20	7.6–32.5	King et al. (1999)
T. s. tetrataenia	♀ 515.0 ♂ 416.0	0.23	23.1	Halstead et al. (2011)

Tail injuries and predation pressures

Tail pseudoautotomy functions as an anti-predator defense mechanism allowing snakes to escape predation attempts (Slowinski and Savage 1995; Fitch 2003; Todd and Wassersug 2010) and tail injuries and loss has often been used as to indicate high local predation pressures (Mushinsky and Miller 1993; Placyk and Burghardt 2005; Sparkman et al. 2013). Yet, recent alternative theoretical and empirical studies assert tail injuries are due to predator inefficiency or other factors (Schoener 1979; Medel et al. 1988; Bowen 2004), which should be considered in interpreting predation effects. High predation pressure has been suggested as the source of in *T. eques*, as well as am increase risk of mortality, but this inference has been based on correlation from studies with low sample sizes. Rosen and Schwalbe (1988) suggested that broken and damaged tails seen in *T. eques* were caused by "relentless predatory pressure of bullfrogs", but we did not find evidence to support this at BP where bullfrogs are abundant. The proportion of *T. eques* with tail injuries at BP (11.1%) is similar to data from other Arizona sites with bullfrogs (13.7%) and without bullfrogs (16.8), suggesting bullfrogs may not be the major cause of tail loss in *T. eques* (Table 11). Furthermore, *T. eques* tail injury frequency in Arizona is comparable to other North American *Thamnophis* (18.5%), and other aquatic snakes such as *Nerodia* and *Regina* (23.3%) (Table 12) that occur within the native and non-native range of bullfrogs (e.g., Placyk and Burghardt 2005).

Table 11. Missing tail rates comparison among Arizona *T. eques* populations. *Before bullfrog introduction.

Site	Missing tail frequency (*n*)	Bullfrogs Present	Source
Big Sandy River	9.0 % (22)	No	AZGD
Bill Williams River	11.1% (18)	Yes	AZGD
BPFH	11.1% (321)	Yes	This study
Dead Horse S.P.	11.1% (45)	Yes	Nowak et al. unpubl
Finley Tank	19.3% (31)	No	d'Orgeix 2011
Santa Cruz	14.2% (189)	Yes	AZGD
Santa Maria	4.5% (21)	No	AZGD
Tucson	46.6% (15)	No*	AZGD, unpubl specimen review
Tonto Creek	14.2% (105)	Yes	Nowak et al. unpubl
Tuzigoot	23.8% (42)	Yes	Emmons et al. 2016
Scotia Canyon	0.0% (13)	No*	Holm & Lowe 1995
Scotia Canyon	23.0% (39)	Yes	Holm & Lowe 1995
Scotia Canyon Total	17.3% (52)		
All Sites Total	14.2% (866)		
Total with bullfrogs	13.7% (742)		
Total without bullfrogs	16.8% (125)		

We also found no evidence that tail loss or injury affected snake body condition, and surprisingly, adult females and males exhibited similar frequency of tail injury, a finding unique in *Thamnophis*. For example, females experience greater tail loss frequency than males in *T. s. parietalis* (Fitch 1999), *T. sirtalis*, and *T. sauritus* (Willis et al. 1982), which has been attributed to reduced mobility and increased predator exposure while basking during gestation (Seigel et al. 1987; Mushinsky and Miller 1993). However, the lack of a sex difference in tail injury frequency suggests that male and female *T. eques* at BPFH face similar predation exposure and escape rates, or a difference may be obscured by our smaller male sample sizes. Bullfrogs are capable of causing injuries to snakes during predation attempts, and in 2009 at BP we captured a healthy *T. eques* with an old mid-body scar that formed a half-moon scar consistent with a failed bullfrog attack (Fig 17), but to our knowledge there are no direct observations of bullfrogs causing tail loss or injuries in *T. eques*. Further work on the behavior of the snakes and their predators at BPFH will help determine predation risk and patterns.

Table 12. Tail injury frequency (%) comparison among other *Thamnophis* species and aquatic snakes with similar ecology to *T. eques*. Values for *T. eques* are summed from across all Arizona sites, total includes unidentified sex and differs from sex specific values. Sample size in parentheses.

Species	Tail injury frequency	♂	♀	Source
Nerodia clarkii	32.7 (110)	42.8 (21)	30.3 (89)	Mushinsky & Miller 1993
N. cyclopion	22.9 (179)	19.7 (71)	25.0 (108)	Mushinsky & Miller 1993
N. erythrogaster	17.4 (86)	10.3 (29)	21.1 (57)	Mushinsky & Miller 1993
N. fasciata	15.2 (233)	15.1 (73)	14.4 (160)	Mushinsky & Miller 1993
N. rhombifer	19.5 (448)	18.4 (223)	14.2 (225)	Mushinsky & Miller 1993
N. sipedon	10.0 (220)	11.3 (62)	9.8 (133)	Bowen 2004
Regina grahamii	43.7 (80)	32.1 (28)	50.0 (52)	Mushinsky & Miller 1993
Thamnophis butleri	12.0 (251)	8.0 (148)	14.0 (139)	Willis et al. 1982
T. eques	14.2 (866)	12.8 (257)	18.1 (364)	This study
T. sauritus-1	9.5 (502)	7 (251)	12 (288)	Willis et al. 1982
T. sauritus-2	15.0 (346)	NA	NA	Todd & Wassersug 2010
T. sirtalis-1	17.9 (940)	14.6 (416)	20.4 (524)	Fitch 1965
T. sirtalis-2	16.7 (886)	10.3 (399)	16.7 (487)	Fitch 2003
T. sirtalis-3	19.0 (523)	NA	NA	Placyk & Burghardt 2005
T. sirtalis-4	9.6 (685)	6.0 (370)	13.0 (413)	Willis et al. 1982

Figure 17 Adult T. eques *with a bite scar from an apparent failed bullfrog predation attempt. Photo by Valerie L. Boyarski.*

We caution attributing *T. eques* tail injuries to bullfrogs in the absence of direct observations because it can distract from understanding pressures from other predatory species or other causes.

For instance, wading birds and raptors are a large source of tail injury to *T. elegans* (Sparkman et al. 2013) and *Nerodia* spp. (Mushinsky and Miller 1993), and corvids (e.g., crows and ravens) are major predators on *T. sirtalis* (Shine et al. 2001). At BP it is common to see numerous wading birds that are known snake predators such as Great Blue Herons (*Ardea herodias*), Green Herons (*Butorides virescens*), Snowy Egrets (*Egretta thula*), and Cattle Egrets (*Bubulcus ibis*) foraging along the edges of the hatchery ponds, as well. Common Black Hawks (*Buteogallus anthracinus*) perched on trees scanning the hatchery grounds for prey. All of which have been observed preying on snakes at BP on multiple occasions (e.g., Fig 18). In addition, tail loss and injuries can occur from non-predation factors caused from frost damage (Amiel and Wassersug 2010) and trematode and nematode parasites (Uhrig et al. 2015). We suggest further studies using snake models or observation studies, wading bird foraging and attack behaviors on snakes as well as an investigation on parasites to better quantify tail loss in *T. eques*. Such approaches will provide managers to better assess strategies to mitigate risk if they are deemed problematic.

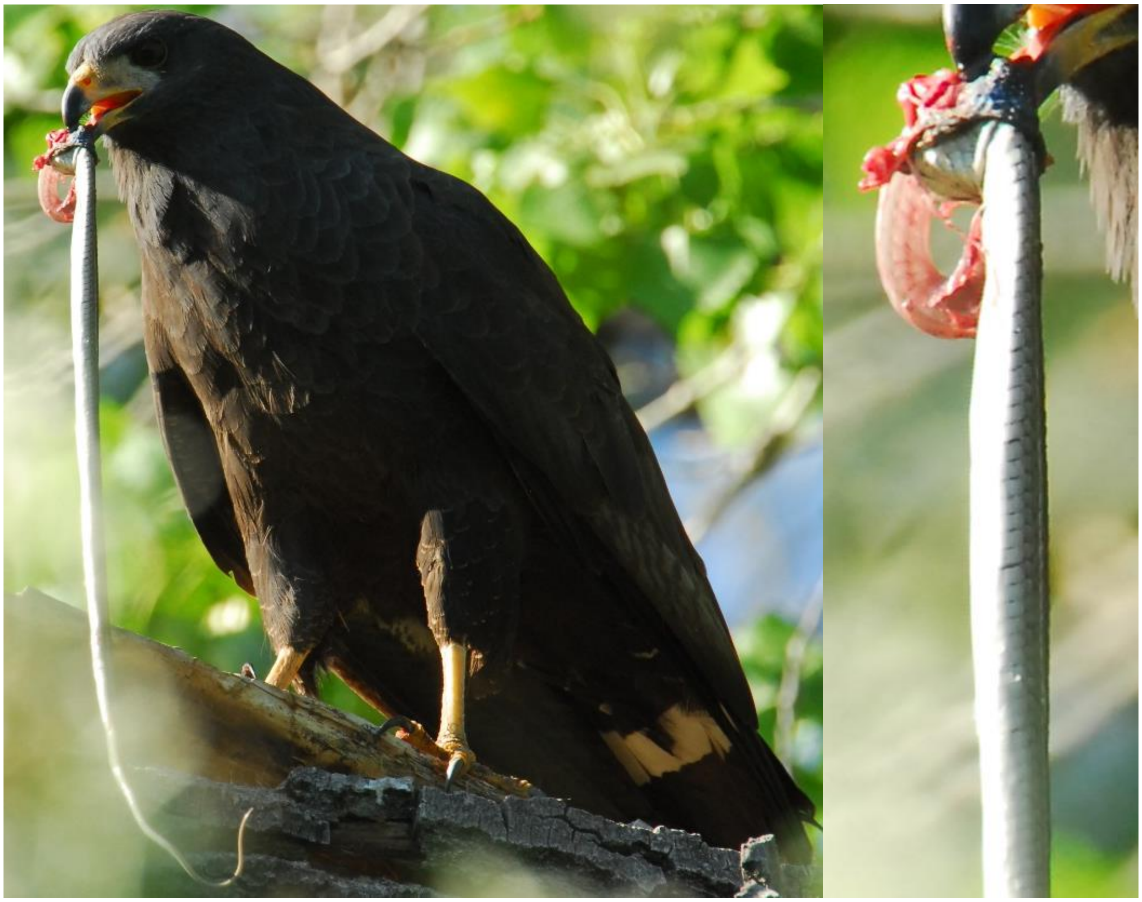


Figure 18. A common Black Hawk preying on a T. eques at BP on 28 April 2011. Image on the right is zoomed in on the snake showing dorsolateral stripe and scale rows. Photo by George Andrejko.

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APPENDIX

The information presented below consists of novel and important natural history miscellany from this project.

A1. *Growth rate & longevity*: Using our growth rate calculations, we estimate that male *T. eques* at BPFH reach sexual maturity by age 2–3 and females by age 3–4, which is consistent with Rosen and Schwalbe's (1988) estimate for *T. eques*, and in other gartersnake species (Carpenter 1952; Bronikowski and Arnold 1999; Rose et al. 2018). The general growth rate of *T. eques* at BPFH concurs with other snake studies in that young males grow faster than females, but our estimates can be improved with more accurate length measurements, larger sample sizes, and fitting von Bertalanffy's growth curves to identify age- and sex-specific asymptotes (Bronikowski and Arnold 1999).

There is little information on the life span of wild *Thamnophis* with estimates for only a few species, but in captivity longevity ranges can be up 17 years for T. elegans (Tacutu et al. 2018). To our knowledge longevity estimates of wild species are known for *T. marcianus* (7 years; Robert et al. 2007), *T. sirtalis parietalis* (9 years; Rollings et al. 2017), *T. elegans* (>15 years; Sparkman et al. 2007). Here we report estimated longevity for *T. eques* calculated from snakes captured during this effort and snakes recaptured by Tiffany Sprague in 2016.

On 13 September 2007 a 447 mm SVL male (snake PIT tag ID P01528) was captured and on 9 April 2016 (captured by Tiffany Sprague) this snake was recaptured at a length of 656 mm SVL. Mean neonate SVL at BPFH is 183 mm SVL, and we used this measurement as the length at year 0. Annual male neonate growth rate is 173 mm SVL, so we estimate that by year 1 this snake would have been a juvenile at 356 mm SVL. Annual male juvenile growth rate is 124 mm SVL and by the end of year 2 would be 480 mm SVL. According to these estimates we infer that this snake was born in 2005, making it 9 years old in 2016.

On 24 Jun 2009 a 500 mm SVL female (snake PIT tag ID P60651) was captured and on 26 September 2016 (captured by Tiffany Sprague) this snake was recaptured at 821 mm SVL. Annual neonate female growth rate is 153 mm SVL and we estimate this snake was 346 mm SVL at year 1. Annual female juvenile growth rate is 110 mm SVL, and by the end of year 2 it would have been 456 mm SVL, and would have reached 500 mm SVL in year 3, 2009. Thus we estimate this snake was born in 2006, making it 10 years old in 2016.

A2. *Diet*: Over the course of the study 32 *T. eques* regurgitated prey while being held for processing (Table A1). These observations show *T. eques* consumes mainly amphibians and fish, the most abundant resources, at BP. Amphibians were the most abundant prey, and non-native bullfrogs are important prey item, similar to the *T. eques* on the Verde River (Emmons et al. 2016).

We had prey mass and snake mass for 13 individuals and percentage of prey/snake mass ranged from 2–46%. The animal that consumed 46% of its mass was a 227 mm SVL, 15 g neonate that ate 7 metamorphic *Bufo* sp. There was no difference in the proportion of fish to amphibians consumed by month ($P = 0.6415$, $\chi^2 = 0.88$) and no difference among age classes ($P = 0.6162$, $\chi^2 = 0.96$).

Table A1. Summary of *T. eques* prey items recorded from BPFH during this study. $^{+}$larval stage; *tadpoles from single snake; **observed eating an unidentified snail species, another *T. eques* died while eating a nonnative Chinese Mystery Snail (*Cipangopaludina chinensis*; Young and Boyarski 2012) and is not excluded here

Prey Species or group	# of stomachs	% of stomachs	Total prey items	% of diet
Ambystoma mavortium^{+}	2	6	3	3
Bufo punctatus*	1	3	4	4
B. woodhousii*	1	3	21	24
UNID *Bufo*	2	6	12	13
Juvenile	1	3	3	3
Tadpole	1	3	9	10
All *Bufo* sp.	4	12	37	42
Juvenile	1	3	3	4
Tadpole	3	9	34	38
Rana catesbeiana	17	54	28	31
Juvenile	14	42	15	17
Tadpole	4	12	13	14
Total Amphibians	23	72%	77	79%
Fish	8	24	18	20
Snail**	1	3	1	1

A3. Species list of amphibian and reptile species from Bubbling Ponds Fish Hatchery Complex.

Scientific name	Common name	Status/Notes
Amphibians (4)		
Salamanders (1)		
Ambystoma m. mavortium	Barred Tiger Salamander	
Frogs & Toads (3)		
Bufo punctatus	Red-spotted toad	
Bufo woodhousii	Woodhouse’s toad	
Rana catesbeiana	American Bullfrog	Non-native
Reptiles (13)		
Lizards (4)		
Aspidoscelis uniparens	Desert grassland whiptail	
Aspidoscelis velox	Plateau striped Whiptail	
Elgaria kingii	Madrean Alligator Lizard	
Sceloporus clarkii	Clark's Spiny Lizard	
Snakes (8)		
Diadophis punctatus	Ring-necked Snake	
Lampropeltis getula	Common Kingsnake	
Masticophis flagellum	Coachwhip	
M. taeniatus	Striped Whipsnake	
Pitupohis catenifer	Gopher Snake	
Thamnophis eques	Northern Mexican Gartersnake	State & Federally Protected
Crotalus atrox	Western Diamond-back Rattlesnake	Venomous
Crotalus molossus	Black-tailed Rattlesnake	Venomous
Turtles (1)		
Kinosternon sonoriense	Sonora Mud Turtle	