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Growth, Survival, and Reproduction in a Northern Illinois Population of the Plains Gartersnake, *Thamnophis radix*

KRISTIN M. STANFORD AND RICHARD B. KING

A six-year mark-recapture study, consisting of 567 captures of 216 individually marked snakes, and the birth of 889 young in 53 litters born to 39 wild-caught females were used to estimate demographic and life-history parameters of a Northern Illinois population of *Thamnophis radix*. Using the von Bertalanffy growth model, males were found to differ from females in asymptotic size but not in the rate at which they approached this size. Size of known age individuals together with growth rate estimates were used to assign age at first capture. Age and sex were then used as grouping variables to obtain age- and sex-specific survival using program MARK. The results suggest that males and females have approximately equal survival in the 0 and 1 age classes but that females have higher survival than males as adults (0.45 vs 0.35). Population estimates calculated using Schumacher-Eschmeyer and Jolly-Seber methods indicate an adult population size of 64 and 172 adults, respectively, corresponding to densities of 40 and 107 adults per hectare. Average female fertility increased from 6.4 in one-year-old females to 21 among six-year-old females. Detailed demographic studies such as this have utility in development of management strategies and theories concerning life-history evolution.

DETAILED demographic data constitutes the underlying framework for understanding the ecology and life history of all species. Among reptiles, demographic studies have often focused on lizards and have resulted in a thorough understanding of the ecology of many of these animals (Huey et al., 1983; Vitt and Pianka, 1994; Pianka and Vitt, 2003). However, demographic studies of their close relatives, the snakes, have struggled to obtain similar results. The secretive nature of many snakes together with low population densities can lead to recapture rates too low for a thorough mark-recapture study (Parker and Plummer, 1987). This has led some authors to question snakes' suitability for in-depth demographic studies (Turner, 1977; Plummer, 1985b). Despite these shortcomings, snake population ecology has been the focus of numerous recent studies (e.g., Brown and Weatherhead, 1999b; Diller and Wallace, 2002; Blouin-Demers et al., 2002). Furthermore, many snakes are listed as vulnerable, threatened, or endangered by state or federal agencies (Levell, 1998; Gibbons et al., 2000) and reliable demographic data on these or related species will likely prove invaluable in their management and recovery (Dodd, 1987, 1993).

Garter snakes are model organisms for the study of snake ecology because of their wide distribution and local abundance (Rossman et al., 1996). The Plains Gartersnake, *Thamnophis radix*, is a diurnal, medium-sized gartersnake (380–710 mm SVL) that mates in April or May and gives birth to 5–60 young from August to

early October. It ranges from southeastern Minnesota and eastern Iowa through southern Wisconsin and northern Illinois to northwestern Indiana, with remnant populations occurring in north-central Ohio, southwestern Illinois, and central Missouri. This species is commonly found in river valleys and near prairie ponds, primarily feeding on earthworms, slugs, and small amphibians (Conant and Collins, 1998; Phillips et al., 1999; Walley et al., 2003). *Thamnophis radix* reaches exceedingly high densities compared to other *Thamnophis* species (Seibert, 1950; Reichenbach and Dalrymple, 1986; Rossman et al., 1996), making it an attractive species for population studies.

In this study, we examine the demographic parameters of a Northern Illinois population of *T. radix* using six years of mark-recapture data. Parameters include sex-specific growth and age structure, sex- and age-specific annual survival and capture probability, population size and density, and sex- and age-specific reproductive characters. Of these parameters, annual survival is perhaps of greatest interest (Lebreton et al., 1992). Accurate estimates of survival are rare for snakes but are central to development of management plans for threatened or endangered species (Dodd, 1987, 1993) and to understanding life-history evolution (Dunham et al., 1988). Sex and age (or size) are factors most commonly included in analyses of survival among snakes. Several authors have found differences in survival between sexes (e.g., Seibert and Hagen, 1947; Feaver, 1977; Forsman, 1995), among age

classes (e.g., Jayne and Bennett, 1990; Forsman, 1993; Brown and Weatherhead, 1999a), or both (e.g., Brown and Parker, 1984; Baron et al., 1996; Plummer, 1997). In this study, we assume that sex and age affect survival in *T. radix* by allowing for separate parameter estimates among age classes and between sexes. By including sex and age as factors in the models explored, we can begin to understand the effects these variables may have on population dynamics.

MATERIALS AND METHODS

Study site.—A 2.65-ha study site was located on the campus of Northern Illinois University (NIU) along the banks of the Kishwaukee River in DeKalb, Illinois. This site is bordered by a paved bicycle path and residential lawns and is maintained by NIU, the city of DeKalb, and individual landowners. From 1995–2001, field surveys were conducted in which snakes were hand captured, measured to obtain snout–vent length (SVL), uniquely marked by clipping ventral scales (Brown and Parker, 1976), and released. A total of 216 snakes were captured 567 times over the entire study. Of these captures, 425 occurred between 1999 and 2001 when more frequent surveys were conducted.

Growth rate.—The integrated, nonlinear form of the von Bertalanffy equation was fit to data collected between 1995 and 2000: Current SVL = $A - [(A - \text{prior SVL}) \times e^{-k \times t}]$.

In this equation, A is the asymptotic body size, and k is the characteristic growth rate at which a snake approaches this size (Dunham, 1978). To estimate these two parameters, we used an iterative, nonlinear-regression process provided in SPSS (vers. 10.1). Parameters were calculated separately for males and females. Growth was also calculated as the difference in SVL between captures divided by the interval in days (t) spent growing: Daily Growth Rate = (current SVL – prior SVL)/ t .

An annual active season of 212 days was determined by the earliest (17 March) and latest (15 October) observed capture dates. Because snakes grow only during the active season, growth intervals that spanned two or more seasons were adjusted by subtracting the number of inactive days. Examination of scatter plots of growth rate versus mean SVL revealed no difference between estimates based on multiple captures within a season and between seasons, and hence, within- and between-season capture intervals were pooled. Growth rate was com-

pared between males and females using ANCOVA with mean SVL as a covariate.

Large individuals sometimes appeared to decrease in SVL between captures within a year presumably because of measurement error. To minimize this error, only first and last captures within a season were used to calculate growth rate for an individual snake. This also reduced the lack of independence among growth rates resulting from multiple measures for the same animal (Brown and Weatherhead, 1999b). Still, negative within-season growth of up to 7% was observed for some snakes. This implies an error of up to 7% in measures of SVL and so both positive and negative growth increments of less than 7% were omitted for within-season captures. Other authors have omitted negative growth increments from analyses of growth rate (e.g., Brown and Weatherhead, 1999b), whereas some have included all measures in their analysis (e.g., Blouin-Demers et al., 2002). However, because both small negative and positive increments likely reflect measurement error, the technique used here should provide conservative, but more accurate, estimates.

Age estimation.—To relate body size to age, Van Deventer (1978) integrated the linear form of the von Bertalanffy equation: Age = $(1/k) \times \ln(-A \times k + k \times \text{SVL}) + c$.

Both A and k are defined as before, and c is the constant of integration and can be determined using a snake's size at a known age. Size at birth is useful for this purpose. Mean size at birth was 138.4 mm SVL, and mean date of birth was 9 August (see Results). This date was used as a starting point for the newborn age class (Age class 0), which consisted of snakes \leq 54 days (9 August to 15 October). To calculate c , mean size at birth (138.4 mm) was substituted into the age equation along with parameter estimates of A and k . Equations for males and females were calculated separately and growth curves were generated relating age to SVL.

Age estimates obtained using this equation were modified in two ways. First, because this equation estimates age in "growth days" or number of active days a snake could have grown, from 0–6 winter seasons (up to 918 days) were added to the "growth days" (e.g., 153 days was added to the age of a snake whose age was 54–266 growth days, to account for 1 winter season). Second, ages were adjusted up or down (whichever required a smaller adjustment) to give a birth date of 9 August. The final estimate of age was the difference in days between this estimated birth date and date of capture.

Among the growth data examined here, 51

individuals were captive born and, therefore, of known age. For these snakes, age estimation was not necessary, but provided an indication of the match between estimated and true age. Some known age individuals (1995, 1996, and 1999 cohorts) were maintained in captivity between 36 and 52 weeks before being released, whereas others (1998 and 2000 cohorts) were released within two weeks after birth. Scatter plots of captive-reared animals ($n = 28$) versus those immediately released ($n = 22$) indicated that the captive reared animals were similar in size to snakes of the same age that had been released at birth and so were included in the analyses presented here. Additionally, some female snakes were held captive for up to 21 weeks prior to and following parturition. Their growth rates were similar to those of similar-sized females from the field. To be conservative, we conducted separate analyses excluding these females but found no significant difference between the two analyses.

Snakes were assigned to age classes by dividing their estimated age in days by 365 and rounding to the nearest whole number (0–6). There were four female snakes that exceeded the estimated asymptotic length at initial capture and, therefore, could not be aged using the age equation. Based on female snakes of similar size, these snakes appear to have been in their fifth year or higher.

Survivorship.—Using age-class and sex as grouping variables, age- and sex-specific survival (Φ) and capture (p) parameters were estimated in the program MARK (White and Burnham, 1999). Data sets were modeled as “recaptures only” using default options for the link function and variance estimation (White and Burnham, 1999). This data type uses the basic Cormack-Jolly-Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965). A few individuals ($n = 9$) that were found dead or that were euthanized because of an injury were excluded from analysis. To test whether parameter estimates varied from year to year, saturated global models, specifying either time dependence (t) or constancy (c) among the years, were examined using the small sample version of the Akaike Information Criterion (AICc). This analysis revealed that constant survival and capture probability among years, $\Phi_c p_c$, best fit the data and resulted in a 20-parameter model (10 survival and 10 recapture probabilities for two sexes and five age classes). To test for overdispersion and goodness-of-fit (GOF), the bootstrap GOF test provided within MARK was implemented and revealed that overdispersion was low ($P = 0.38$; $df = 12$).

Additionally, mean expected deviance (deviance_{exp} = 87.13) calculated from 100 simulations was close to observed deviance of the global model (deviance_{obs} = 90.34), yielding an overdispersion factor close to one ($\hat{c} = 1.04$).

Once the global model was established, simpler models (e.g., equal male and female survivorship in each age class) were explored using AICc. Models were constructed using different combinations of parameter index matrices (PIMs) for survival and recapture parameters ($n = 19$ and 17 matrices, respectively; for matrix structure, see Stanford, 2002). Matrices were created by allowing differential equality among the initial 20 parameters in the global model, although still maintaining biological integrity (Burnham and Anderson, 1998). Models were also compared using Akaike weights, which examine how well a particular model is supported when compared to other models. Finally, model averaging, in which models with lowest Akaike weights contribute the most to parameter estimates, was used over the entire model set.

Population size.—To facilitate comparisons of adult (age-classes 2–4+) population size and density with previous estimates for *T. radix*, both the Jolly-Seber and Schumacher-Eschmeyer methods (Caughley, 1977; Krebs, 1989) were applied to the mark-recapture data from the year 2000. This year had the most captures, allowing for the most accurate assessment of population size to be made (Koper and Brooks, 1998). Separate estimates were also computed for males and females because of potential differences in catchability between sexes and to minimize error (Krebs, 1989; Koper and Brooks, 1998). Population densities were determined by dividing the estimated population size by the size of the study area. To test whether marking had an effect on catchability, data were compared to a zero-truncated Poisson distribution (Caughley, 1977; Plummer, 1985b) prior to population estimation.

Reproduction.—Size and age at sexual maturity were estimated from observations of courtship, mating, offspring production, and presence of sperm in cloacal smears (Fitch, 1987). Gravid females were captured and held in captivity for 1–13 weeks prior to parturition. Snakes were individually housed in 40-liter aquaria and were provided with shelter, water ad libitum and earthworms 2–3 times per week during gestation. Offspring were sexed, measured, and weighed within 48 h of birth. Some of the offspring ($n = 196$) were maintained in captivity between 36 and 52 weeks after birth. These in-

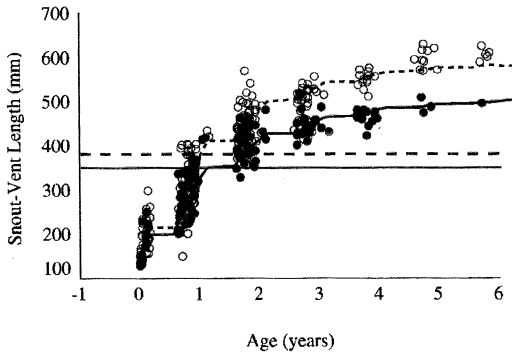


Fig. 1. Growth curves for male (solid symbol and line) and female (open symbol and dashed line) *Thamnophis radix*. For age classes 0–2, only subsets of data points are shown. Plateaus in the curves indicate time spent over-wintering in which animals were assumed to not grow.

dividuals were also individually housed and provided water ad libitum and earthworms 2–3 times per week while in captivity before being released. Others were marked and released within two weeks of birth. A total of 53 litters were born to 39 different females (eight females had two litters, and three females had three litters).

Mean age-specific female fertility was determined from 46 litters. Seven other litters were excluded because they were incomplete (palpitation indicated that some fetuses remained unborn) or consisted of a single malformed offspring. Linear regression was used to examine the relationship between female SVL and number of offspring following natural logarithm transformation (King, 2000). Mean age-specific fertility for females from each year-class was determined from the intersection of the expected SVL at the mean birth date of 9 August with this regression line. Age-specific female fecundity was then calculated by multiplying the expected number of offspring produced by the age-specific female survivorship.

RESULTS

Growth rate.—We obtained 164 growth increments for 120 snakes (70 males, 50 females), including 96 within-season increments, 57 spanning two consecutive field seasons, and 11 spanning three or more field seasons. The von Bertalanffy model provided a good fit to the observed change in SVL (males: $r^2 = 0.93$; females: $r^2 = 0.94$; Fig. 1). Males and females differed in asymptotic SVL (males: $A = 502.3$, 95% confi-

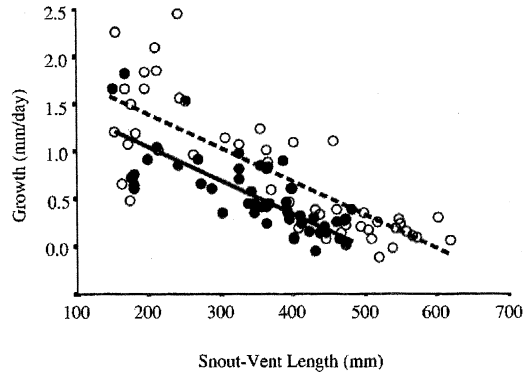


Fig. 2. Daily growth rate vs. snout-vent length for male (solid symbol and line) and female (open symbol and dashed line) *Thamnophis radix*.

dence interval = 472.0–532.7; females: $A = 582.0$, 95% confidence interval = 545.9–618.0; confidence intervals do not overlap) but not in growth rate (males: $k = 0.0033$, 95% confidence interval = 0.002–0.004; females: $k = 0.0035$, 95% confidence interval = 0.003–0.004; confidence intervals do overlap). Following Plummer (1997), we attempted to validate the estimated asymptotic SVL by examining SVL of the 20 largest males and females in the population. Mean SVL of the largest females was close to the predicted asymptotic length (mean = 584.75 mm, range 555–628). Mean SVL of the largest males was 19 mm below the predicted asymptotic length (mean = 483.10 mm, range 469–519). Analysis of covariance of daily growth rate with sex as a factor and mean SVL as a covariate, gave similar results to those obtained using the von Bertalanffy model (Fig. 2, Table 1). The relationship between daily growth rate and mean SVL did not differ between sexes in slope ($F_{1,96} = 0.91$, $P = 0.343$; Table 1A) but did differ in intercept ($F_{1,97} = 24.04$, $P < 0.001$; Table 1B).

Age estimation.—Initially, seven age classes (Age 0–Age 6) were identified for both sexes (Fig. 3). However, because of low sample sizes in older age groups, age classes 4 through 6 were pooled for survivorship analyses. For 51 captive-born individuals, a plot comparing estimated age with true age and indicated there were few ($n = 3$) cases where an animal had been misclassified (following Plummer, 1997). Two of these individuals had inflated growth rates that were calculated over two or more seasons, causing over-estimation of age. The other individual was unusually large for its age, resulting in an estimat-

TABLE 1. ANCOVA OF DAILY GROWTH RATE WITH SEX AS A FACTOR AND MEAN SVL AS A COVARIATE, TESTING FOR EQUALITY OF SLOPES (A) AND INTERCEPTS (B).

Source	Sum of squares	df	Mean square	F	P
A.					
Sex × SVL	0.104	1	0.104	0.907	0.343
Sex	0.665	1	0.665	5.819	0.018
SVL	14.905	1	14.905	130.338	<0.001
Error	10.978	96	0.114		
B.					
Sex	2.747	1	2.747	24.044	<0.001
SVL	18.485	1	18.485	161.803	<0.001
Error	11.082	97	0.114		

ed age one year older than its true age. Overall, comparisons of estimated and known ages indicate that most snakes were classified into the correct age classes.

Survivorship.—We examined 81 models based on the 20 parameter global model of constant survival and capture ($\Phi_c p_c$) across years. Twelve of the 81 models had similar AICc values and were considered to be equally parsimonious under the criterion of Burnham and Anderson (1998; Table 2). All of these models indicated that survival varied with age and sex (see also

Stanford, 2002). Examination of the Akaike weights showed slightly more support for one model (18–17; Table 3). However, this support was not strong enough to disregard other models and model averaging was used to generate estimates based on all models in the dataset (Fig. 4).

When survival parameters were averaged among models, males and females had similar survival as neonates and as juveniles (male age-class 0 = 0.17; female age-class 0 = 0.16; male age-class 1 = 0.42; female age-class 1 = 0.41). Female survival then increased to 0.52 in age-class 2, while male survival remained unchanged (male age-class 2 = 0.42). Both sexes decreased in survival in older age-classes (male age-classes 3–4+ = 0.35–0.37; female age-classes 3–4+ = 0.44–0.45; Fig. 4A). Model-averaged capture probabilities varied among age classes but not between sexes. The highest probability of capture occurred in age-class 3 and the lowest in age-class 4+ (Fig. 4B). Averaged estimates were age-class 0 = 0.52, age-class 1 = 0.56, age-class 2 = 0.42, age-class 3 = 0.66, age-class 4+ = 0.35.

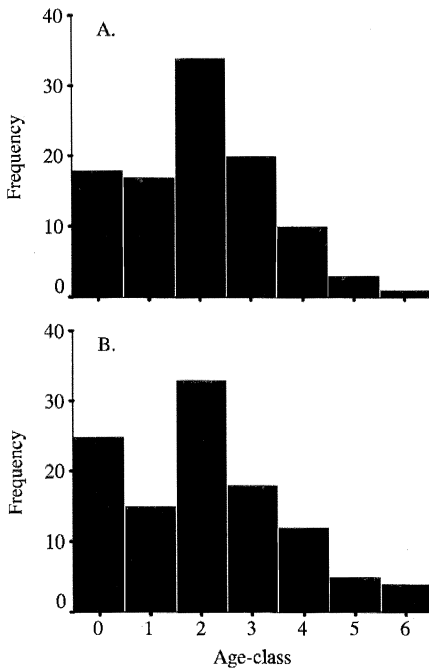


Fig. 3. Frequency histograms showing the observed number of male (A) and female (B) snakes in each year-class between 1995 and 2000.

Population size.—The zero-truncated Poisson test for equal catchability using data collected in 2000 indicated no difference in capture probability between newly captured and previously marked animals ($\chi^2 = 4.5$, $df = 3$, $P > 0.05$). The Jolly-Seber method gave a total adult population size of 172.5, as well as separate estimates for males (68.2) and females (113.0) within the study site (Table 4). Population size estimates generated using the Schumacher-Eschmeyer method indicated a total population size of 64.1 adults with 31.4 males and 35.3 females (Table 4). Density estimates using both the entire study site and just the south half (1.61 ha), where approximately 90% of our captures

TABLE 2. ESTIMATES OF SURVIVAL (A) AND CAPTURE (B) PARAMETERS FOR MALE AND FEMALE *Thamnomphis radix* FOR EACH OF THE 12 BEST-FIT MODELS TOGETHER WITH WEIGHTED AVERAGES AND 95% CONFIDENCE INTERVALS. Weighted averages were calculated based on the AIC value from each model. Models with the lowest AICs contribute the most to the averaged estimate. Separate parameter estimates are provided for males (M) and females (F) for those models in which sexes were treated separately. Otherwise, a single parameter estimate is show for males and females combined.

Model	Age 0		Age 1		Age 2		Age 3		Age 4+		
	M	F	M	F	M	F	M	F	M	F	
A.											
18-17	0.16		0.42		0.35	0.53	0.35	0.53	0.35	0.53	
18-3	0.16		0.42		0.35	0.54	0.35	0.54	0.35	0.54	
18-1	0.16		0.42		0.31	0.52	0.31	0.52	0.31	0.52	
4-17	0.16		0.42			0.46		0.46		0.46	
4-3	0.16		0.42			0.46		0.46		0.46	
1-1	0.16		0.42			0.53		0.30		0.30	
19-17	0.16		0.45	0.38	0.35	0.53	0.35	0.53	0.35	0.53	
19-3	0.16		0.45	0.38	0.35	0.54	0.35	0.54	0.35	0.54	
17-1	0.16		0.42			0.53	0.21	0.40	0.21	0.40	
2-1	0.16		0.42		0.41	0.60		0.30		0.30	
18-2	0.16		0.42		0.35	0.52	0.35	0.52	0.35	0.52	
18-12	0.19		0.41		0.35	0.53	0.35	0.53	0.35	0.53	
Weighted average	0.17	0.16	0.42	0.41	0.42	0.52	0.35	0.44	0.37	0.45	
95% Confidence Interval	0.07-0.33	0.07-0.33	0.29-0.56	0.28-0.55	0.21-0.67	0.32-0.71	0.17-0.59	0.23-0.68	0.16-0.64	0.21-0.71	
B.											
18-17	0.55		0.55			0.45		0.45		0.45	
18-3	0.55		0.49			0.49		0.49		0.20	
18-1	0.55		0.55			0.45		0.82		0.21	
4-17	0.55		0.55			0.43		0.43		0.43	
4-3	0.55		0.55			0.45		0.45		0.21	
1-1	0.55		0.55			0.34		—		0.34	
19-17	0.55		0.55			0.45		0.45		0.45	
19-3	0.55		0.55			0.49		0.49		0.20	
17-1	0.55		0.55			0.35		—		0.29	
2-1	0.55		0.55			0.37		—		0.34	
18-2	0.55		0.55			0.44		0.51		0.51	
18-12	0.43		0.57			0.45		0.45		0.45	
Weighted average	0.52	0.56	0.56	0.42	0.42	0.42	0.66	0.66	0.35	0.35	
95% Confidence Interval	0.24-0.80	0.33-0.76	0.33-0.76	0.21-0.67	0.21-0.67	0.21-0.67	0.14-0.96	0.14-0.96	0.07-0.79	0.07-0.79	

TABLE 3. NORMALIZED AKAIKE WIGHTS (w) OF THE BEST-FIT MODELS AFTER THE USE OF AICc. Support values indicate how well a given model is supported relative to other models tested.

Models tested	Akaike weights (w)	Support
18–17 vs 18–3	0.0674 \div 0.06215	1.1
18–17 vs 18–1	0.0674 \div 0.05532	1.2
18–17 vs 4–17	0.0674 \div 0.04836	1.4
4–17 vs 4–3	0.04836 \div 0.03457	1.4
18–3 vs 4–3	0.06215 \div 0.03457	1.8
18–17 vs 4–3	0.0674 \div 0.03457	2.0
18–1 vs 17–1	0.05532 \div 0.02739	2.0
18–1 vs 2–1	0.05532 \div 0.02627	2.1
18–17 vs 19–17	0.0674 \div 0.02997	2.2

occurred (Stanford, 2002), gave values ranging from 24.2 to 107.1 adults/ha.

Reproduction and fecundity.—Observed occurrences of courtship ($n = 6$) and mating ($n = 6$) involved males ranging from 406–480 mm SVL and females ranging from 433–588 mm SVL. Cloacal smears were examined for the presence of sperm from males ranging from 257 mm to 519 mm SVL ($n = 163$) and females ranging from 235 mm to 628 mm SVL ($n = 101$). Sperm was found in smears from 35 males collected between 2 April and 29 August and from 20 females collected between 6 April and 5 June. Additionally, sperm was found in one female collected on 1 September, suggesting that a fall mating had occurred. Among free-ranging snakes, the smallest male and female with sperm measured 355 mm and 380 mm SVL, respectively.

The smallest gravid female collected was 389 mm SVL but produced only one stillborn offspring. Females that produced live offspring ($n = 48$) ranged from 458 mm to 635 mm SVL. Based on observations of courtship and mating, offspring production, and presence of sperm, reproductive maturity appears to be reached be-

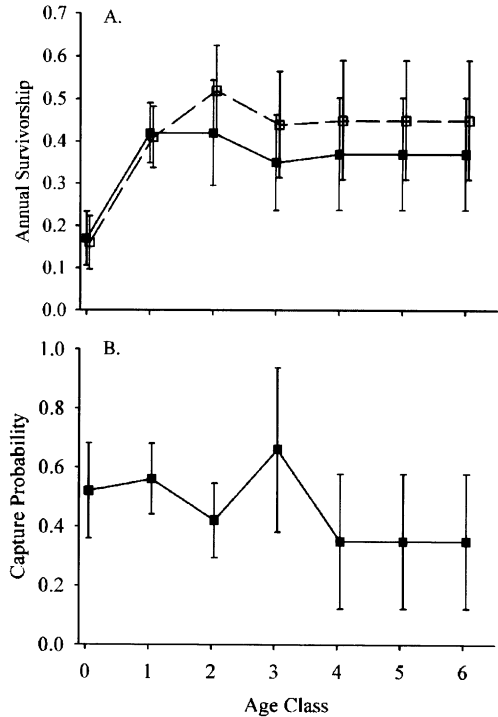


Fig. 4. Model averaged estimates of male (solid symbol and line) and female (open symbol and dashed line) age-specific survival (A) and capture probabilities (B), including their corresponding standard errors. Capture probabilities were equal for males and females.

tween 350 and 370 mm SVL in males and 380 and 400 mm SVL in females. This corresponds to age class 2 for most individuals (Fig. 1).

The proportion of female offspring was not different from 50% (binomial test normal approximation, $Z = 1.05$, $P = 0.29$). Mean offspring SVL was 138.4 mm and did not differ significantly between males and females ($F_{1,483} = 0.81$, $P = 0.775$) but did differ among litters ($F_{37,483} = 21.13$, $P < 0.001$) based on ANOVA with sex as a factor and litter as a block effect.

TABLE 4. POPULATION SIZE AND DENSITY ESTIMATES FOR *Thamnophis radix* USING BOTH JOLLY-SEBER AND SCHUMACHER-ESCHMEYER TECHNIQUES. Densities were calculated using the entire site as well as a smaller section of the site within which 90% of all captures occurred (values in parentheses).

	Jolly-Seber Estimates			Schumacher-Eschmeyer Estimates		
	Population size	95% Confidence interval	Density (per ha)	Population size	95% Confidence interval	Density (per ha)
All adults	172.5	(106.4–402.6)	65.1 (107.1)	64.1	(42.2–132.6)	24.2 (39.8)
Males	68.2	(38.4–212.5)	25.7 (42.4)	31.4	(17.9–125.9)	11.8 (19.5)
Females	113.0	(54.0–422.8)	42.6 (70.2)	35.3	(19.3–209.8)	13.3 (21.9)

TABLE 5. MEAN NUMBER OF OFFSPRING PRODUCED BY *Thamnophis radix* FEMALES FOR EACH YEAR AND EACH AGE-CLASS.

	# of litters	Mean # offspring	Range
Year			
1995	3	11.7	10–15
1996	3	23.3	21–27
1998	8	20.3	13–29
1999	14	18.5	10–30
2000	12	18.5	9–31
2001	6	18.2	14–20
Age-class			
1	1	4.0	—
2	23	17.0	9–27
3	11	18.2	10–30
4	9	20.0	10–27
5	1	30.0	—
6	2	30.0	29–31

Number of offspring per female averaged 18.4 (range = 4–31) but varied among years and age-classes (Table 5). Linear regression revealed a significant positive relationship between the total number of offspring and female SVL ($F_{1,44} = 16.366$, $P < 0.001$, $r^2 = 0.271$; Fig. 5). Mean age-specific fertility was determined from the intersection of expected female SVL on 9 August for each age class and the regression line (Fig. 5; Table 5). Age-specific female fecundity was then calculated by multiplying the age-specific fertility and the age-specific female survival (Table 6). This method of fecundity calculation assumes no mortality between the time of breeding and the census period (Akçakaya et al., 1999).

TABLE 6. AGE-SPECIFIC FERTILITY AND FECUNDITY ESTIMATES FOR *Thamnophis radix*. Age at the mean birthdate (9 August) was used to calculate expected female SVL using the modified form of the age equation. The expected number of offspring was then determined using the regression equation. Age-specific fecundity was calculated assuming a postbreeding matrix by multiplying the age-specific fertility by the corresponding female survivorship.

Female Age class	Age (in days) at mean birthdate	Expected female SVL (mm)	Expected number of offspring (fertility)	Female survival	Age-specific fecundity
1	145	314.16	6.44	0.41	2.64
2	357	453.92	13.22	0.52	6.87
3	569	520.75	17.29	0.44	7.61
4	781	552.71	19.42	0.45	8.74
5	993	567.99	20.49	0.45	9.22
6	1205	575.30	21.01	0.45	9.45

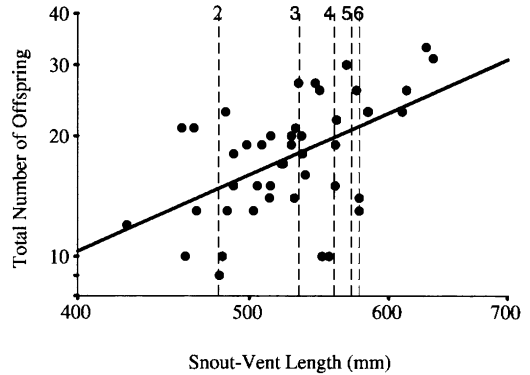


Fig. 5. Total number of offspring versus female snout-vent length in *Thamnophis radix* (both variables plotted on log scales). The regression equation $\ln(\text{total \# offspring}) = -9.379 + 1.955 * \ln(\text{SVL})$ was used to determine the expected number of offspring for each age-specific mean female snout-vent length (vertical dashed lines).

DISCUSSION

Growth rate and age estimation.—As for many reptiles, the von Bertalanffy model accurately describes growth in *T. radix*. Males and females had the same characteristic growth rate but grew to different asymptotic sizes, indicating that absolute growth rate is higher in females than in males (Tables 1, 2). This pattern is similar to that seen in the Northern Watersnake, *Nerodia sipedon* (Brown and Weatherhead, 1999b). However, because growth can vary greatly among populations within species (Bronikowski and Arnold, 1999), it may be important to investigate other populations of *T. radix* to better understand growth in this species.

Differences in growth rate between males and

females play a major role in sexual-size dimorphism in adult body size (Shine, 1990, 1993, 1994). Rates of juvenile growth can influence dimorphism in two ways (Andrews, 1982). Juveniles can grow at the same rate until the smaller of the two sexes draws close to asymptotic size, after which size diverges as the larger sex continues to grow (e.g., *Ophedryx aestivus*, fig. 2 in Plummer, 1985a). Alternatively, males and females may grow at different rates starting early in life as is likely the case in *T. radix*. Figure 1 depicts divergence in size early in life and suggests that growth rate of juvenile female *T. radix* is higher than that of males (see also Fig. 2). Seibert and Hagen (1947) found that females exceeded males in growth rate during the first two years of life; however, age groups in that study were determined from size-frequency distributions, a method that has serious limitations (Caughley, 1977; Halliday and Verrell, 1988). As sample sizes of known-age juveniles increase, the length and degree to which juvenile *T. radix* growth may differ between the sexes can be addressed.

Using the von Bertalanffy model, seven age classes were identified in the NIU Plains Gartersnake population, suggesting that *T. radix* may survive 6–7 yr. This is consistent with the average longevity (~ 6.7 yr) of early-maturing colubrids reported in Parker and Plummer (1987). Because age was based on a continuous morphological character, it is likely that there is some error in age assignment (Caughley, 1977). Plummer (1985a) found that the probability of error in aging snakes increases for older age classes. His conclusion that age estimates were most accurate for the first two years likely applies to this study as well (Fig. 1). Some error may arise from inaccuracy in growth rate estimates. For example, few males achieved asymptotic size (Fig. 1), suggesting that the true asymptote may be somewhat lower. Alternatively, this lack of large males may be because of low survival (35%) and capture probability (35%) of the oldest age classes. Individual variation in growth trajectories and asymptotic size also likely contributes to error in age assignment. This source of variation remains virtually uninvestigated in reptiles. Inclusion of known-age individuals should have reduced error in age assignment in this study. Corroboration of our age estimates using skeletochronology (Waye and Gregory, 1998; Waye, 1999) is in progress.

Survivorship.—Using MARK, the best-fit global model indicated constant survival and capture probability ($\Phi_{c,p}$) over years in this study. Although some studies have found annual varia-

tion in survival (e.g., Brown and Parker, 1984; Plummer, 1997; Diller and Wallace, 2002), others report that annual survival was constant (Flatt et al., 1997; Brown and Weatherhead, 1999b). Other variables that could affect survival and capture parameters in *T. radix* include food availability (Platt, 1984), predation (Plummer, 1990), precipitation (e.g., Brown and Parker, 1984), winter severity (Feaver, 1977; Gregory, 1977) and mowing intensity (Dalrymple and Reichenbach, 1984). The scope of this study did not include determining whether such extrinsic factors affect survival in *T. radix*. However, because all of these factors are likely to vary from year to year, the lack of time-dependence in the global model suggests their impacts are small.

Capture probabilities in the NIU population of *T. radix* were found to be dependent on age but not on sex. The estimates fluctuate up and down; however, the confidence intervals are rather broad (Fig. 4). It seems reasonable that the probability of capture should be lowest among the oldest animals (age-class 4+); however, it is unknown why the probability of capture would be lower in age-class 2 (42%) than in age-classes 1 or 3 (56% and 66%). Results from the analysis of reproduction indicated that most males and females reach sexual maturity by their second year. Therefore, it may be that behavioral changes associated with the onset of reproduction could account for the decrease in the probability of capture in age-class 2.

Annual survival varied with age and sex in the NIU population of *T. radix*. Males and females were similar in survival as neonate and as juveniles (age-classes 0 and 1), but adult survival was higher in females than in males (Fig. 4). Seibert and Hagen (1947) also found female survival to be greater than male survival in *T. radix* in both the first- and second-year age groups of their study but again, their age groups were determined from size-frequency distributions. Plummer (1985a, 1997) used the same aging technique as in this study and also found average adult female survival to be higher (41%) than that of adult males (28%) in *Ophedryx aestivus*.

Adult female annual survival of the NIU population of *T. radix* was greater than that of neonates (age-class 0) and juveniles (age-class 1; Fig. 4). In a study of a related species, Brown and Weatherhead (1999a) found a strikingly similar pattern for age-specific female survival in *N. sipedon*. They estimated neonate survival (age-class 0) to be 20%, juvenile survival (age-class 1) to be 41%, age-class 2 survival to be 61%, and age-class 3 survival to be 64% in age-class 3. Survival decreased to 48% in older age

classes (age-classes 4–9), and survival did not differ between sexes within age-classes.

In their review, Parker and Plummer (1987) report average annual adult survival is 50% in early-maturing colubrid snakes, 70% in late-maturing colubrids, and 75% in late-maturing viperids. Thus, adult survival in *T. radix* appears similar to other early maturing colubrids. First-year survival was also reported in Parker and Plummer's (1987) review. However, most authors give only crude estimates based on number of expected offspring produced compared to the number of one-year-olds observed the following year. Overall, survival in the first year for most colubrids was low (mean \approx 26%) compared to that of most viperids (Parker and Plummer, 1987). *Thamnophis radix* also has low neonate survival (16%) but higher first-year survival (41%).

Population size and density.—Population size estimates give an adult population size of 64.1 (Schumacher-Eschmeyer method) and 172.5 adults (Jolly-Seber method), yielding approximate densities of 40 and 107 adults per hectare, respectively. Some criticism of the accuracy of these population estimators has been raised by Koper and Brooks (1998). Specifically, they noted that both methods often underestimated the true population size in *Chrysemys picta*, especially when sample sizes were low. However, they also point out that both the Schumacher-Eschmeyer and Jolly-Seber estimates were closer to estimating the true population size when the largest samples were used. By limiting our analysis to the year with the greatest sample size, these methods should be providing us with the best estimates of population size and density for further comparison.

The density estimates reported here are similar to those calculated by Reichenbach and Dalrymple (1986) for an endangered Ohio population (52–123 snakes/ha). Other estimates for this species are markedly higher (e.g., 845 snakes/ha in Seibert and Hagen, 1947 and Seibert, 1950; 320 snakes/ha in B. Bauerle, 1972, unpubl. report). Reichenbach and Dalrymple (1986) suggested that the high densities reported by Seibert (1950) could have resulted from the highly disturbed condition of the study site. However, the site investigated by B. Bauerle (1972, unpubl.) was apparently relatively undisturbed. Comparisons among species show that even low density populations of *T. radix* are denser than most *Thamnophis* species (table 4-3 in Rossman et al., 1996; table 9-1 in Parker and Plummer, 1987, table 6 in Reichenbach and Dalrymple, 1986). Other snakes that reach high

densities are usually small, secretive species such as *Diadophis punctatus*, *Ophedrys aestivus*, and *Regina alleni* (Parker and Plummer, 1987). For a snake of its size, the Plains Gartersnake occurs in densities an order of magnitude greater than other *Thamnophines* of similar size. The reasons for this phenomenon are still unknown and deserve further investigation.

Reproduction and fecundity.—A combination of evidence suggests that male and female *T. radix* reach sexual maturity at 350–370 mm and 380–400 mm SVL, respectively. These sizes correspond to most snakes reaching sexual maturity at two years of age (Fig. 1). There were two cases in which a female in her first year (age-class 1) produced offspring, but both litters were small and mostly stillborn, indicating that females that attempt to reproduce in their first year are probably not very successful at it. Because of trade-offs between growth and reproduction (Shine, 1980; Roff, 1992; Shine and Schwarzkopf, 1992), female *T. radix* may benefit by allocating energy to growth rather than reproduction during their first year of life.

The presence of sperm in cloacal smears of males from early spring through the fall indicates that sperm production is postnuptial, with maximal spermatogenic activity in late summer and early fall (Seigel and Ford, 1987), as in other garter snakes (Rossman et al., 1996). Postnuptial reproductive cycles are sometimes associated with both spring and fall mating (e.g., Fitch, 1965; Gregory, 1977) and the presence of sperm in a female in September provides evidence of fall mating in *T. radix* (also see Pope, 1964). However, sperm in fall samples of both male and female *T. sirtalis* are sometimes nonmotile (Gregory, 1977).

Average litter size for the NIU population of *T. radix* was 18.4. This is somewhat higher than the average litter size reported previously for Illinois (13.3) but falls well within the range of reported means across regions (e.g., Fitch, 1985; Seigel and Fitch, 1985; Rossman et al. 1996). The overall primary sex-ratio of offspring in the NIU population of *T. radix* did not differ from 1:1. This is consistent with what is known for most snake species (Parker and Plummer, 1987). However, the ratio of male to female offspring has been reported to vary with female size (Lemen and Voris, 1981; Dunlap and Lang, 1990; Weatherhead et al., 1995). Mean offspring SVL was found not to differ between male and female *T. radix* but did differ among families. Family, sex, and geographic differences in neonate size have previously been reported for related species (e.g., geographic in *T. sirtalis*,

Gregory and Larsen, 1993; family and sex in *N. sipedon*, Weatherhead et al., 1995; family and sex in *S. dekayi*, King, 1997). Additional analyses are necessary to determine whether family effects in *T. radix* are influencing the demographic parameters reported here.

Female SVL and litter size were positively correlated but only weakly so ($r^2 = 0.27$, $n = 46$). A comparably weak correlation was observed for *T. radix* in Missouri ($r^2 = 0.22$, $n = 52$; table 8.2 in Seigel and Ford, 1987). A stronger correlation between SVL and litter size has been reported in some viviparous snakes (e.g., Ford and Seigel, 1989; Brown and Weatherhead, 1997), but as in *T. radix*, this relationship is weak in others (e.g., Fitch, 1965; King, 1986; Seigel and Ford, 1987). Factors other than body size can affect the number of offspring produced (e.g., female condition at ovulation, King, 1993; food availability Andren and Nilson, 1983; see also Dunham et al., 1988). Recently, Bonnet et al. (2003) demonstrated that the strength of the correlation between SVL and litter size is sensitive to sampling bias. In particular, they suggest that strong correlations result only in years or samples consisting of females with high relative clutch mass.

The intersection of female size at the mean parturition date and the regression line relating litter size and SVL provided an estimate of expected age-specific fertility. When compared to observed mean litter sizes, expected values are lower, especially in the older age-classes (age-classes 5 and 6). This could be, in part, caused by small sample size for older age classes. However, even among females in age-class 2 ($n = 23$ observed litters), the observed mean litter size was 17, whereas the expected value from the regression was 13.2. Examination of Figure 5 suggests that moderate-sized females sometimes produced unusually small litters. Because estimated age is based on body size (SVL), error in age-specific fecundity may be inflated based on compounding error. The effects of body size and age on fecundity may become better understood as the number of known age animals increases in the population.

Information gained from studies such as this can be used to determine which parameters most strongly influence population trends (see Stanford, 2002). Often, understanding how and to what degree demographic parameters influence a population is more useful than the estimates themselves (Caswell, 2000b). Knowledge gained from demographic studies can be used to develop management strategies for the population under study or for populations with similar life-history characteristics (e.g., Heppell et

al., 2000; Caswell, 2000a; Webb et al., 2002). Specifically, data from this study are currently being used to develop a recovery plan for the endangered population of *T. radix* in Ohio (KMS, 2003, unpubl. report). However, care must be taken in generalizing across species and even populations because of variability in life-history parameters (e.g., Oostermeijer et al., 1996; Silvertown et al., 1996; Heppell, 1998). Because detailed demographic data are often lacking for threatened and endangered species, generalizations based on well-studied populations such as the one described here can provide valuable information regarding the effectiveness of such management tools as head-starting and augmentation.

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