

## DEMOGRAPHY OF AN URBAN POPULATION OF RING-NECKED SNAKES (*DIADOPHIS PUNCTATUS*) IN MISSOURI

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**Abstract.**—Snakes are generally considered poor subjects for studies of population and community ecology because of low recapture rates and high variability in density and survival estimates. Some species, though, can be found seasonally in large numbers and thus may be good model organisms for life-history studies. I conducted a capture-mark-recapture study on an urban population of Ring-necked Snakes (*Diadophis punctatus*) in Jefferson City, Missouri, USA over three years to determine population structure and growth rates. I divided the population into three age classes: Year 1, Year 2, and Adult ( $\geq 3$  y of age). Survivorship varied depending on age, but recapture probabilities were low across all age classes. Less than half of the population was predicted to survive to reach 3 y of age, although a  $\lambda$  value of 1.23 signified a growing population. Sensitivity of age classes suggests that population trajectories are reliant upon recruitment of year-class two individuals into their third year of life.

**Key Words.**—age; life tables; population growth rates; sensitivity analyses

### INTRODUCTION

Small, secretive snake species can occur in relatively high densities and thus make up a significant portion of biomass in areas which they occur (Fitch 1975; Godley 1980; Wilson and Dorcas 2004). In spite of serving as an integral part of local ecosystems, many snake species are understudied and lack basic life-history information (Parker and Plummer 1987; Seigel 1993). Demographic vital rates can be difficult to estimate when studying cryptic species, as estimates may not accurately reflect actual values driving the trajectory of a population. Deviations of estimated demographic rates in some snake species are most likely influenced by low recapture rates (Plummer 1985). Most studies that have quantified critical life stages of snakes have focused on larger species such as *Enhydryna* (Voris and Jayne 1979), *Acrochordus* (Houston and Shine 1994), *Nerodia* (Brown and Weatherhead 1999) and *Elaphe* [*Pantherophis*] (Blouin-Demers 2002), with little work published on smaller, more fossorial species.

Snakes are generally considered poor subjects for studies on population and community ecology because of low recapture rates and high variability in density and survival estimates (Turner 1977; Parker and Plummer 1987; Vitt 1987). Seigel (1993) argues that problems associated with studying snake populations are an artifact of matching question, technique, and species. Development of baseline ecological information for many species then is dependent upon testing and implementing methodologies appropriate for sampling a particular species of interest. Fitch (1975; 1999) reported finding large numbers of Ring-necked Snakes (*Diadophis punctatus*) during the spring months in northeastern Kansas under rocks, coverboards, and

sheets of metal, and reported densities ranging from 923–1374 snakes/ha. A concurrent demographic study of Western Worm Snakes (*Carphophis vermis*) reported densities of 119/ha, further demonstrating that secretive subterranean snakes could be sampled adequately with an understanding of habitat requirements and application of adequate techniques (Clark 1970; Fitch 1999).

Even less is known about the impacts of urbanization on demographic vital rates of snakes. Urbanization results in destruction and conversion of natural lands to commercial, industrial, and residential land uses (Berry 1990), and as a result is responsible for habitat loss and population declines for many species of amphibians and reptiles (Hamer and McDonnell 2008; Mitchell and Brown 2008). Some smaller species of snakes though, could be considered urbanophiles (Rodda and Tyrrell 2008) due in part to their small size and ability to tolerate and even capitalize on human alterations to their natural habitat. Some species, such as Ring-necked Snakes and Northern Brown Snakes (*Storeria dekayi*), thrive in disturbed areas that are littered with refuse and or downed vegetation (Meshaka 1999; Gaul 2008).

To better understand the impacts of urbanization on the life history of snakes, comparative studies between wild and urban populations are obviously needed (Mitchell and Brown 2008), but the dearth of information on snake life-histories makes any comparative study difficult. To build upon the baseline information present for Ring-necked Snakes, I conducted a mark-recapture study in Jefferson City, Missouri, USA, to determine the population structure, survivorship, and population growth rate of Ring-necked Snakes in an urban environment.



**FIGURE 1.** Photographs of the study plot showing debris along the fence line separating a wood plot and adjacent vacant lot in Jefferson City, Missouri USA. (Photographed by J. Daren Riedle).

### MATERIALS AND METHODS

The study site was located on the Lincoln University campus, immediately adjacent to McClung Park, Jefferson City, Missouri, USA. I sampled a linear 500 m<sup>2</sup> (7.5 × 66.7 m) plot four times in 2011, six times in 2012, and three times in 2013, between March and May to coincide with the time of year when snakes are most likely to occur under surface debris (Fitch 1975). The sample plot demarcated a border between a 5-ha wood plot and a 1-ha vacant lot, and was defined by human debris that had been dumped along the wood line (Fig. 1). I sampled the site by using the debris left along the wood line as cover objects, and I captured snakes basking or resting just underneath. The study site was surrounded by university campus and residential neighborhoods. I determined the sex of all Ring-necked Snakes captured using a cloacal probe, and I recorded snout to vent length (SVL: mm), tail length (mm), and mass (g). I marked individual snakes using medical cautery units (Aaron Medical Change-A-Tip cautery units; Aaron Medical, St. Petersburg, Florida, USA; www.boviemedical.com; Winne et al., 2006). I branded one to four ventral scales using a marking scheme described by Blanchard and Finster (1933).

Fitch's (1999) demographic study of Ring-necked

Snakes was of much longer duration and he was able to identify three age classes based on SVL. As his study site was close to mine and at the same latitude, I adopted his year classes under the assumption there would be little variation between sites. First-year males were ≤ 146 mm SVL and first year females were ≤ 159 mm SVL. Second-year males were 147–214 mm and second-year females were 160–220 mm. After the second year, Fitch (1975) reported that growth rates slowed and were quite variable across both age and sex, so snakes ≥ 3 y of age were labelled adults. Adult males were ≥ 215 mm SVL and adult females ≥ 221 mm SVL. Blanchard et al. (1979) reported similar age and growth results for a population of Ring-necked Snakes in northern Michigan. While there may likely be variation in age and growth in my population, these earlier studies do provide important baseline data for demographic analyses used in this study.

I examined sex ratio to determine if it deviated significantly from 1:1 for all three age classes using a Chi-square test ( $\alpha = 0.05$  for all tests used). I tested for sexual size dimorphism by comparing the mean SVL, tail length, and mass using a *t*-test. Recapture and demographic vital rates were calculated using encounter histories derived from capture-mark-recapture data in Program MARK (White and Burnham 1999). I calculated population size, apparent survival (assuming constant survivorship for each of the three age classes), and recapture rates using open population Cormack-Jolly-Seber (CJS) and POPAN models in Program MARK (Lebreton et al., 1992; White and Burnham 1999) and I assumed constant survival and recapture rates.

When using encounter histories to calculate demographic traits, you are estimating the probability that an individual will leave a population. If the encounter rates are reversed, then one can estimate the probability of an individual entering the population (Pradel 1996). In doing so you can estimate  $\lambda$ , where  $\lambda$  = rate of individuals entering a population or cohort. This differs from a traditional calculation of  $\lambda$  where the population growth rate is derived as a dominant eigenvalue from a projection matrix model. So the  $\lambda$  estimated using Pradel models only estimates the realized growth rates of the age class from which the encounter rates were generated but is not necessarily equivalent to the growth rate of the population. To avoid confusion with other analysis, I referred to these values as Pradel's  $\lambda$  in this manuscript. Pradel's  $\lambda$  was estimated by Program Mark in conjunction with the CJS model described above.

I constructed a vertical life table (Pianka 1994) for the first 15 years of life for this population of Ring-necked Snakes. I used age specific apparent survivorship values calculated in Program MARK to calculate ( $l_x$ ). The life table was based on females only, and I applied

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survivorship values for adult age classes for all 3–15 y old snakes. Even though growth was considerably variable in snakes > 3 y old, Fitch (1975) did provide size ranges for snakes up to 15 y of age. Clark et al. (1997) reported size specific fecundity data for a population of Ring-necked Snakes in Maryland and noted their results were similar to that of Fitch (1975). Using size and fecundity data calculated by Fitch (1975) and Clark et al. (1997), in combination with sex-ratios derived from my study population, I calculated fecundity where  $m_x$  = the number of female offspring produced by each female.

Once I calculated fecundity values for each age class, net reproductive rate ( $R_0$ ) or average number of age class zero offspring produced by an average newborn organism during its lifetime could be calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x$$

Generation time for this population was then defined by:

$$T = \sum_{x=\alpha}^{\omega} x l_x m_x / R_0$$

Finally, I also calculated the contribution of a given age group to the next generation between age and death, or reproductive value (Fisher 1930). Reproductive value was defined as:

$$v_x = \sum_{t=x}^{\infty} \frac{l_t}{l_x} m_t$$

A combination of the reproductive value of age classes and calculation of Pradel's  $\lambda$  do provide useful mechanisms for identifying age classes that maybe most sensitive to change. Another tool in analyzing critical life stages are population viability models, which are traditionally used to predict risk of extinction, expected time of extinction, chance of recovery, and identification of sexes and or age classes most sensitive to perturbation (Akçakaya and Sjögren-Gulve 2000). I constructed a three stage population viability model in RAMAS Metapop (Akçakaya 2002), that included year class 1,

TABLE 1. Male:Female sex ratio and  $\chi^2$  values for Ring-necked Snakes (*Diadophis punctatus*), Jefferson City, Missouri, USA.

	Male: Female Ratio	$\chi^2$	P
Year 1	1:1.33	1.60	0.10
Year 2	1:0.64	1.95	0.10
Adult	1:1.23	0.93	0.50

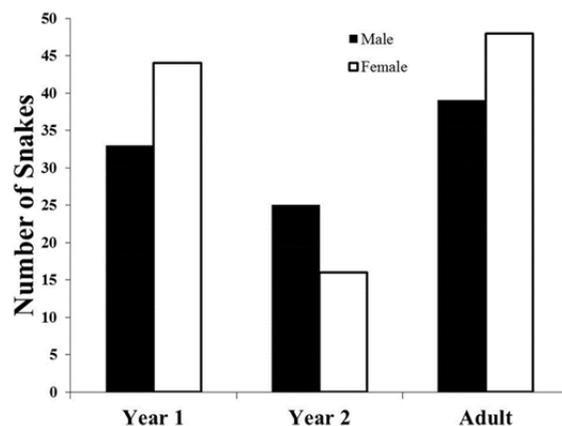


FIGURE 2. Number of male and female Ring-necked Snakes (*Diadophis punctatus*) in year 1, year 2, and adult age classes at an urban study site in Jefferson City, Missouri USA.

TABLE 2. Snout to vent length (SVL: mm), tail length (mm) and mass (g)  $\pm$  1 standard error for adult Ring-necked Snakes (*Diadophis punctatus*), Jefferson City, Missouri, USA.

	Male	Female	P
SVL	244 $\pm$ 2.5	251.5 $\pm$ 3.4	0.05
Tail	56.7 $\pm$ 1.7	48.9 $\pm$ 1.4	<0.01
Mass	6.26 $\pm$ 0.27	6.78 $\pm$ 0.37	0.14

year class 2, and adult Ring-neck Snakes using the demographic information calculated from mark-recapture analysis and reproductive rates derived from the life table. Density dependence type was set as ceiling with a carrying capacity of 1,000 individuals. I set the model to run for 10 time steps (years) and 1,000 iterations.

## RESULTS

I marked 205 individuals and captures of year class 1 and adult snakes were similar, although there were fewer captures of year class 2 snakes (Fig. 2). Sex ratios did not differ significantly from 1:1 for any age class (Table 1). Females had significantly longer SVL and significantly shorter tails than males, although there was no difference in mass between sexes (Table 2). Densities for this population were 188  $\pm$  29 individuals for the 500 m<sup>2</sup> study plot (Table 3).

Apparent survivorship was similar between year class 1 and adult snakes, but lower for year class 2 snakes (Table 3). Recapture probabilities were very low for all age classes (Table 3). Estimates of Pradel's  $\lambda$  were stable for year 1 and adult age classes, but suggested a decreasing year 2 age class (Table 3).

Life table analysis yielded a net reproductive rate of 2.88 and a generation time of 5.71 years with 63% of the population dying before they reach sexual maturity. Age weighted fecundity was highest for 5–6 year old snakes

**TABLE 3.** Apparent survival ( $\Phi$ ), recapture probability ( $p$ ), population size (N) and Pradel's  $\lambda \pm 1$  standard error for Ring-necked Snakes (*Diadophis punctatus*) in Jefferson City, Missouri USA.

Age Class	$\Phi$	$P$	N	Pradel's $\lambda$
Year 1	0.76 $\pm$ 0.12	0.04 $\pm$ 0.03	85 $\pm$ 17	0.99 $\pm$ 0.03
Year 2	0.62 $\pm$ 0.16	0.06 $\pm$ 0.06	380 $\pm$ 215	0.87 $\pm$ 0.04
Adults	0.79 $\pm$ 0.10	0.04 $\pm$ 0.02	188 $\pm$ 29	1.05 $\pm$ 0.02

and reproductive values increased through the first seven years (Table 4).

The  $\lambda$  estimate in RAMAS Metapop for this population was 1.23, suggesting an increasing population. Decreasing survivorship in year class 1 and adult snakes 5–20% yielded no change in  $\lambda$ . Lowering survivorship in the year class 2 snakes by 10% reduced  $\lambda$  to 1.01. A 15% decrease in survivorship created a slightly declining population with  $\lambda = 0.96$  and a 20% decline resulted in  $\lambda = 0.91$ .

**DISCUSSION**

A review of the handful of mark-recapture studies on Ring-necked Snakes suggests a similarity in life history among populations in the northeastern portion of its range, although our understanding of how variation in these traits influences population growth has changed with time. As part of a long-term study in northern Michigan, Blanchard et al. (1979) reported recapturing only 18% of their marked juvenile snakes as adults, but concluded that while recapture rates were low, juvenile survivorship must be high in order for the population to persist. Snakes in the Kansas study reached sexual

maturity at 3 y of age and it was estimated that roughly 50% of each cohort was lost between oviposition and maturity (Fitch 1975; 1999). Life-table analysis for my population projected a 63% decrease in a given cohort in the first three years of life. Survivorship and Pradel's  $\lambda$  values for year class two snakes in my population were low, and fluctuations in survivorship in this age class did influence the trajectory of the population. Fitch (1975) documented fluctuations in the number of year class 1 and 2 snakes captured between years, which he attributed to inter-annual variation in reproduction, hatching success, and survivorship.

Population persistence in Ring-necked Snakes may be most reliant on the transition of juveniles from their second year of life to sexual maturity at 3 y of age, followed by a relatively long life span for adult females. High reproductive values for younger reproductive age classes would be important to ensure adequate and timely recruitment back into the population. Clark et al. (1997) reported a tendency towards larger clutches of smaller eggs, with clutch mass increasing with body size. Both Blanchard et al. (1979) and Fitch (1999) reported recapturing snakes up to 18 y after their first capture, suggesting a relatively long life for a small

**TABLE 4.** Vertical life table including age ( $X$ ), survivorship ( $l_x$ ), fecundity ( $m_x$ ), realized fecundity ( $l_x m_x$ ), age weighted fecundity ( $X l_x m_x$ ), reproductive value ( $V_x$ ), net reproductive rate (R0) and generation time (T) for female Ring-necked Snakes (*Diadophis punctatus*) in Jefferson City, Missouri USA. R<sub>0</sub>=2.88; T=5.71.

$X$	$l_x$	$m_x$	$l_x m_x$	$X l_x m_x$	$V_x$
0	1.00	0.00	0.00	0.00	2.88
1	0.76	0.00	0.00	0.00	3.61
2	0.47	0.00	0.00	0.00	5.97
3	0.37	1.00	0.37	1.11	7.59
4	0.29	1.50	0.44	1.74	8.44
5	0.23	1.75	0.40	2.01	8.76
6	0.18	1.90	0.34	2.05	8.98
7	0.14	2.00	0.28	1.96	9.11
8	0.11	2.10	0.23	1.85	9.08
9	0.09	2.25	0.20	1.82	8.52
10	0.07	2.37	0.17	1.66	8.07
11	0.05	2.37	0.17	1.30	8.02
12	0.04	2.75	0.11	1.13	7.06
13	0.03	2.75	0.08	1.07	5.75
14	0.02	3.00	0.06	0.84	4.50
15	0.01	3.00	0.03	0.45	3.00

species of fossorial snake. Although reproduction in young age classes is important, reproductive contributions from older females may be equally important. This reproductive pattern could best be described as a periodic life-history strategy where environmental variation influencing survival of early life stages is periodic (Winemiller 2005). Essentially reproductive output is allocated across multiple years when variation in juvenile survival is greater than the variation in adult survival. This strategy is reflective of temporal or seasonal heterogeneity of ecosystems, and is considered the dominant strategy observed in fishes, arthropods, mollusks, and plants (Winemiller 1992).

When considering the results from this study though, one should keep in mind the low recapture rates and particularly large standard error for population estimates for year class two snakes. My study site was constrained in size so that I could repeatedly sample the same sub-set of the population. Mean distances moved between captures in the Kansas population was 80 m with activity ranges up to 130 m in diameter, and year class one snakes moved farther than adults (Fitch 1999). Cormack-Jolly-Seber models does not differentiate between emigration and mortality, so results of my study, particularly in the second year class, could be influenced as much by emigration as by mortality.

The demographic characteristics of this urban population of Ring-necked Snakes were similar to that of a geographically close wild population. Ring-necked Snakes exhibit a very general diet feeding upon earthworms, amphibians, small snakes, and lizards (summarized in Werler and Dixon 2000). In the absence of other food items, Ring-necked Snakes will live entirely on a diet of earthworms (Ernst 1962; Myers 1965; and Fitch 1975). This ability to use an abundant food resource in addition to their small size and secretive nature may qualify Ring-necked Snakes as true urbanophiles as defined by Rodda and Tyrrell (2008). What is not known is how the urban matrix impacts distribution and population structure, and whether Ring-necked Snakes are restricted to specific vegetation patches or occur throughout the entire urban matrix (Garden et al. 2006). If Ring-necked Snake distribution is restricted by the patchy nature of an urban environment, then the question of whether demographic values are influenced more by mortality or emigration becomes a bit of a moot point.

The Ring-necked Snake is one of a very few North American snake species with a transcontinental distribution, occupying multiple habitat types and niches (Fontanella et al. 2008), yet few studies have focused on the life history of this species. Results from studies on growth and reproduction in Kansas (Fitch 1975; 1999), northern Michigan (Blanchard et al. 1979), Maryland (Clark et al. 1997), and this study were remarkably similar despite the large geographic distance between

populations. One would expect the life history of the species to vary considerably though in more arid western habitats, as those populations differ considerably in size, diet, and densities (Gehlback 1974; Fontanella et al. 2008). Obviously then, many more studies on the regional demography of Ring-neck Snakes are required to truly understand variation in demographic characteristics throughout their range.

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