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VITAL RATES AND POPULATION DEMOGRAPHICS IN DECLINING AND STABLE WATERSNAKE POPULATIONS

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Abstract.—**Many snake populations have experienced significant declines, including the Copper-bellied Watersnake (*Nerodia erythrogaster neglecta*), a species listed as threatened under the federal Endangered Species Act. Here, we assess aspects of population biology and vital rates in *N. e. neglecta* to help elucidate potential mechanisms of their decline and inform more targeted recovery efforts. We use the Common Watersnake (*Nerodia sipedon sipedon*) as a benchmark for comparison. Survey results indicate that the *N. e. neglecta* population may have experienced a 70% decline in abundance from 2001–2006, whereas the *N. s. sipedon* population remained relatively stable. Annual survivorship rates did not differ appreciably between *N. e. neglecta* (0.67) and *N. s. sipedon* (0.63). Surprisingly, *N. e. neglecta* grew three times faster than *N. s. sipedon*, regardless of sex, with evidence of high growth rates across the entire size-range of the population, suggesting that food resource limitations or excess energy expenditures are not likely constraining *N. e. neglecta*. Frequency of mating encounters, sex ratios, and proportion of juveniles in the sampled population of *N. e. neglecta* showed little evidence of deviation from that of *N. s. sipedon*. While broad scale threats such as habitat fragmentation, the loss of shallow ephemeral wetlands, mining, road mortality, or declines in amphibian prey have likely driven range-wide declines of *N. e. neglecta*, the proximate mechanisms (i.e., fitness consequences) behind the decline of our study population remain unresolved. Nevertheless, the vital rates presented here provide useful information for more informed management and recovery efforts.**

Key Words.—Copper-bellied Watersnake; Common Watersnake; growth; *Nerodia erythrogaster neglecta*; *Nerodia sipedon sipedon*; population declines; radiotelemetry; survival

INTRODUCTION

Reptiles of many species have been recognized as declining due to a number of general causes, including habitat loss and degradation, unsustainable use, invasive species, disease, and climate change (Gibbons et al., 2000), and snakes are no exception (Matthews et al. 2002; Webb et al. 2002; Phillips et al. 2003; Mullin and Seigel 2009). Of particular concern is a recent analysis that identified rapid population declines in several snake populations across multiple continents in both protected areas and those directly exposed to anthropogenic stressors (Reading et al. 2010). In some cases, specific threats or intrinsic attributes of the species in question can be linked to declines (Madsen et. al 1995; Webb and Shine 2000; Webb et al. 2005) or associated with increased vulnerability to stressors (Reed and Shine 2000; Webb et al. 2002). Due in part to their secretive and cryptic nature, the particular suite of threats contributing to population declines in many snake species are complex and not well understood, and will remain enigmatic until more detailed natural history and population studies are completed (Winne et al. 2007).

One common management approach is to examine behaviors such as habitat use, activity, movements, and spatial ecology to determine how changes to the availability and quality of critical habitat influence populations of conservation concern (Roe et al. 2003, 2004). Augmenting such behavioral studies with population surveys allows for an assessment of species response to threats at broader landscape scales (Attum et al. 2008). While this information is critical for conservation practitioners, an assessment of vital rates such as growth, survival, and reproduction can further refine recovery efforts. For example, Row et al. (2007) quantified life-history attributes for *Elaphe obsoleta* and estimated mortality rates from vehicular collision, then used a population viability analysis to forecast local population extirpation in the absence of mitigation measures to increase survival. In another example, consistent declines in reproductive success were empirically linked to inbreeding depression in a small population of *Vipera berus*, and the translocation of males from a nearby location increased genetic diversity and offspring fitness, resulting in population recovery (Madsen et al. 1999). Even when conservation practitioners are generally aware of the broader ultimate causes responsible for population declines (e.g., loss of quality habitat, disease), the proximate mechanisms (e.g., increased mortality, reduced reproduction, reduced growth or body condition) that might be involved often go unobserved.

This lack of knowledge inhibits the development of more targeted, and presumably more successful, conservation and management efforts.

Here, we examine aspects of population demographics and vital rates in two closely-related species, the Copper-bellied Watersnake (*Nerodia erythrogaster neglecta*) and the Common Watersnake (*N. sipedon sipedon*). *Nerodia. e. neglecta* is a subspecies of the Plain-bellied Watersnake (*N. erythrogaster*) that persists only as small isolated populations north of 40° latitude, referred to as the northern population segment and listed as threatened under the federal Endangered Species Act (U.S. Fish and Wildlife Service 1997). *Nerodia. s. sipedon* is relatively common where these two species co-occur (Attum et al. 2008). Previous studies have highlighted behavioral and dietary differences between these species, with *N. e. neglecta* being the more vagile and terrestrial of the two species, and with a specialized diet comprised nearly exclusively of anurans compared to the more generalized diet of aquatic vertebrates of *N. s. sipedon* (Roe et al. 2003; 2004). However, despite the recognition of recent range-wide declines (U.S. Fish and Wildlife Service 1997), no study has detailed population demographic trends in the northern population segment of *N. e. neglecta* to provide information on decline magnitude and rates in localized populations. Moreover, it is not known how or to what extent *N. e. neglecta* and *N. s. sipedon* differ with respect to survivorship, growth, and reproduction: vital rates with population level consequences that may help elucidate potential mechanisms of decline for *N. e. neglecta* or inform more targeted recovery efforts.

MATERIALS AND METHODS

Study site.—We conducted the study in northwestern Ohio and southern Michigan, USA, at a location harboring one of the largest known remaining populations of the northern population segment of *N. e. neglecta* (Attum et al. 2009). The site encompassed nearly 5,000 ha and contained numerous shallow wetlands and small lakes embedded in a terrestrial landscape composed of agricultural fields, mixed deciduous forest, and open fields in various stages of succession. The St. Joseph River also flows through the site. For a more detailed description of the site, see Roe et al. (2003, 2004).

Surveys.—We conducted visual encounter surveys (VES) between 15 April and 15 June at a subset of five wetlands (0.91–3.47 ha area, 384–1110 m perimeter) from 2001–2003, and again from 2005–2006. This time period coincided with high levels of snake activity and optimal visibility prior to full vegetation leaf-out, and we conducted surveys only during weather conditions suitable for observing watersnakes. Each wetland was surveyed at least three times per year. We surveyed by slowly walking the perimeter of the entire wetland and inspecting likely snake habitat, stopping periodically to scan the wetland interior with binoculars. We then mapped survey routes and measured distance traveled to estimate snakes/km as a relative abundance index. Each survey was typically conducted by one trained observer, and on occasions where multiple trained surveyors were involved, survey tracks did not overlap. We identified snakes to species and counted the number encountered, but we did not pursue snakes for capture during formal surveys. Survey duration at each wetland was typically about 40 observer minutes, but this varied depending on the size of the wetland and number of snakes encountered.

Radiotracking.—We radiotracked 35 snakes between May 2001 and October 2002. The sample consisted of 10 female and eight male *N. e. neglecta*, and 10 female and seven male *N. s. sipedon*. Initial snout-to-vent length (SVL) ranged between 52.5 and 111.0 cm for *N. e. neglecta* females, between 61.5 and 82.0 cm for *N. e. neglecta* males, between 54.6 and 82.5 cm in *N. s. sipedon* females, and between 51.0 and 58.0 cm in *N. s. sipedon* males. We used transmitter models SB-2, SI-2, and AI-2 (Holohil Systems Ltd., Carp, Ontario, Canada) ranging in size from 4–28 g representing 1.3–5.8% of the individual's body mass. We surgically implanted transmitters while snakes were under anesthesia using the technique described by Roe et al. (2003).

We located snakes at least once every two weeks during the active season (April–October) and less frequently during overwintering (November–March). At each location, we determined the snake's status as alive, dead, or unknown. If a snake was confirmed dead after an extended period of unknown status (i.e., underground or water, signal not detected), then we assumed it had been dead since the last confirmed visual observation or movement. We also determined whether the snake was engaged in mating activity at each encounter. We captured snakes periodically and measured them for growth determination.

Capture-mark-recapture.—We conducted a capture-mark-recapture study between April 2000 and June 2003. We captured snakes in minnow traps and opportunistically by hand as part of other activities (e.g., during radiotracking). Upon capture, for both species we measured snout-to-vent length (SVL) and body mass of each individual and assessed sex by examining tail length and morphology, as well as by probing. We also implanted all encountered *N. e. neglecta* with a passive integrated transponder (PIT) tag and immediately released them at their point of capture. Because of funding limitations, we did not PIT tag *N. s. sipedon*, so they could not be identified by individual.

Statistical analyses.—We performed statistical analyses with SPSS 17.0 (SPSS Inc., Chicago, Illinois, USA), the program MARK 5.0 (White and Burnham 1999), and SAS 9.2 (SAS Inc., Cary, North Carolina, USA). Where appropriate, we examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, they were transformed to approximate normal distributions or equal variances. For all tests, $\alpha = 0.05$.

We estimated maximum likelihood survival probabilities for radiotracked individuals using known fate models in the program MARK (White and Burnham 1999). We started with a fully saturated model in which survival probability was dependent on species, sex, and time, with initial SVL as a covariate (Table 1). Due to small sample sizes in the demographic groups, we also ran a separate set of models where sexes were grouped and survivorship was dependent on only species and time, including initial SVL as a covariate (Table 2). For each model set, we then fit a series of reduced-parameter models (Tables 1 and 2) and used corrected Akaike Information Criterion (AICc) to rank candidate models; if competing models had AICc values of < 2.0, we considered them as having some support (Lebreton et al. 1992). We assessed fate at bi-weekly intervals during the active season (19 April–25 October) and at a single interval during hibernation (26 October–18 April), defined as the period between the final date of autumn ingress and first spring emergence of either species. Our inability to assess fate while snakes were underground necessitated the longer overwintering time interval (Roe et al. 2010). We censored time periods when radiosignals could not be detected (i.e., transmitter failure or undetected long-distance movements) from the analysis. We derived all estimates by model averaging. We extrapolated annual survival as (survival probability per interval)^{14}, where the exponent is the number of time intervals over the year (13

Table 1. Model results for variability in survivorship probability (*S*) between species and sex over time for Copper-bellied Watersnakes (*Nerodia erythrogaster neglecta*) and Common Watersnakes (*N. sipedon sipedon*). All models include initial snout-to-vent length (SVL) as an individual covariate.

Model	AICc	ΔAICc	Weight	Likelihood	*N*	Deviance
S (species × sex) SVL	140.58	0.00	0.61	1.00	5	130.46
S (·) SVL	142.66	2.08	0.21	0.35	2	138.64
S (sex) SVL	144.32	3.74	0.09	0.15	3	138.27
S (species) SVL	144.47	3.89	0.09	0.14	3	138.42
S (time) SVL	165.40	24.82	0.00	0.00	28	106.05
S (species × time) SVL	215.21	74.63	0.00	0.00	55	91.78
S (sex × time) SVL	216.94	76.36	0.00	0.00	55	93.52
S (species × sex × time) SVL	345.70	205.13	0.00	0.00	109	0.00

Table 2. Model results for variability in survivorship probability (*S*) between species over time for Copper-bellied Watersnakes (*Nerodia erythrogaster neglecta*) and Common Watersnakes (*N. sipedon sipedon*). All models include initial snout-to-vent length (SVL) as an individual covariate. Note that this series of models does not include a demographic variable.

Model	AICc	ΔAICc	Weight	Likelihood	*N*	Deviance
S (species) SVL	144.47	0.00	0.52	1.00	3	138.42
S (·) SVL	144.60	0.13	0.48	0.94	2	142.59
S (time) SVL	165.40	20.93	0.00	0.00	28	106.06
S (species × time) SVL	215.21	70.74	0.00	0.00	55	91.79

bi-weekly active season periods plus one overwintering period).

We examined variation in growth rates of radiotracked snakes using Analysis of Covariance (ANCOVA), with species, sex, and their interaction as the independent variables, $\log_{10}$ SVL growth as the dependent variable, and initial $\log_{10}$ SVL as the covariate. To assess growth rates, we divided change in SVL between captures by the number of days elapsed over the approximately six-month active season. We used Fisher's exact tests to compare the number of individuals exhibiting reproductive behavior between species, comparing only within sex. In the capture-mark-recapture study, we assessed whether sex ratios differed from 1:1 using a Chi-square Test. We examined variation in growth of male and female *N. e. neglecta* using ANCOVA as in the radiotracking study, though with only sex as the independent variable.

RESULTS

Abundance.—Abundance of *N. s. sipedon* relative to *N. e. neglecta* increased over time, with *N. s. sipedon* 1.4 times more abundant than *N. e. neglecta* in 2001 and as much as 7.0 times more abundant than *N. e. neglecta* in 2006. The increasing divergence is attributable to declines in *N. e. neglecta* sightings throughout the study from a maximum of approximately 1.8 snakes per wetland (2.4 snakes/km) in 2001 to as low as 0.5 snakes per wetland (0.6 snakes/km) in 2006 (Fig. 1). In contrast, *N. s. sipedon* relative abundance fluctuated between 2.6 snakes per wetland (3.4 snakes/km) and 6.6 snakes per wetland (8.6 snakes/km), but did not show evidence of decline over the survey period (Fig. 1).

Survivorship.—In the demographic series of models, the model with survival probability incorporating an interaction between species and sex had the most support (Table 1). The strongest differences were between males, with extrapolated annual survival estimates for *N. e. neglecta* males 2.8 times higher than *N. s. sipedon* males, whereas annual survivorship for *N. s. sipedon* females was only 1.2 times that of *N. e. neglecta* females (Table 3). When sex was held constant, models with and without species-specific survival were both supported (Table 2).

Mortality occurred in both active and overwintering seasons (Fig. 2). During the active season (19 April–25 October), bi-weekly survival probabilities ranged between 0.87 and 1.0 for *N. e. neglecta*, and between 0.71 and 1.0 for *N. s. sipedon*. During the overwintering period (26 October–18 April), survival probabilities were 0.83 and 0.87 for *N. e. neglecta* and *N. s. sipedon*, respectively. However, no models with time-dependent

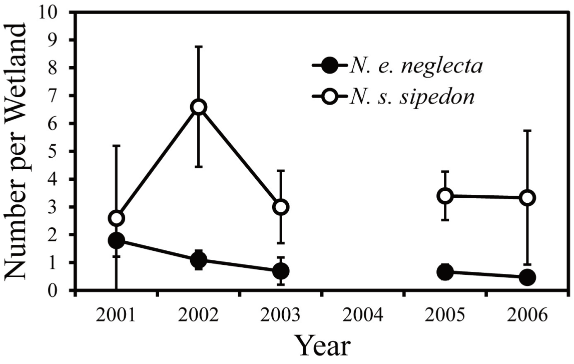

Figure 1. Relative abundance per wetland (mean ± SE) of *Nerodia erythrogaster neglecta* and *N. sipedon sipedon* as determined by visual encounter surveys in five wetlands. Mean survey distance per wetland was 0.765 km.

Table 3. Survivorship estimates for male and female *Nerodia erythrogaster neglecta* and *N. sipedon sipedon* between 2001 and 2003 tracked via radiotelemetry. All estimates were determined by model averaging. Model time intervals were bi-weekly during the active season (19 April–25 October) and condensed to a single interval during hibernation (26 October - 18 April). Annual survival probability was extrapolated as (survival probability per interval)^{14}, where the exponent is the number of time intervals over the year (13 bi-weekly active season periods plus one overwintering period).

		Probability over model interval		Annual probability	
Species	Gender	Estimate (SE)	95% CI	Estimate	95% CI
N. e. neglecta					
	Male	0.983 (0.008)	0.937–0.996	0.787	0.402–0.945
	Female	0.966 (0.015)	0.914–0.987	0.616	0.284–0.833
	Sexes combined	0.972 (0.009)	0.946–0.986	0.672	0.460–0.821
N. s. sipedon					
	Male	0.914 (0.053)	0.598–0.987	0.284	0.001–0.826
	Female	0.976 (0.011)	0.936–0.991	0.712	0.396–0.881
	Sexes combined	0.968 (0.011)	0.936–0.984	0.634	0.396–0.798

variation in survival were supported (Tables 1 and 2).

Growth.—We were able to measure growth rates for four female and three male radiotracked *N. e. neglecta*, and six female and three male *N. s. sipedon*. Intervals between captures ranged from 43–258 active season days. Growth rates depended on body size, and differed between species and sex (ANCOVA SVL: $F_{1,11} = 7.20$, $P = 0.021$; species: $F_{1,11} = 19.5$, $P = 0.001$; sex: $F_{1,11} = 7.68$, $P = 0.018$; species × sex: $F_{1,11} = 1.20$, $P = 0.296$). *Nerodia. e. neglecta* grew faster than *N. s. sipedon*, and females grew faster than males (Fig. 3).

Mating behavior.—Of the radiotracked snakes, 18.2% of female *N. e. neglecta* were observed mating, while mating behavior was observed in 37.5% of male *N. e. neglecta*. For *N. s. sipedon*, 50.0% and 57.1% of females and males, respectively, were observed mating.

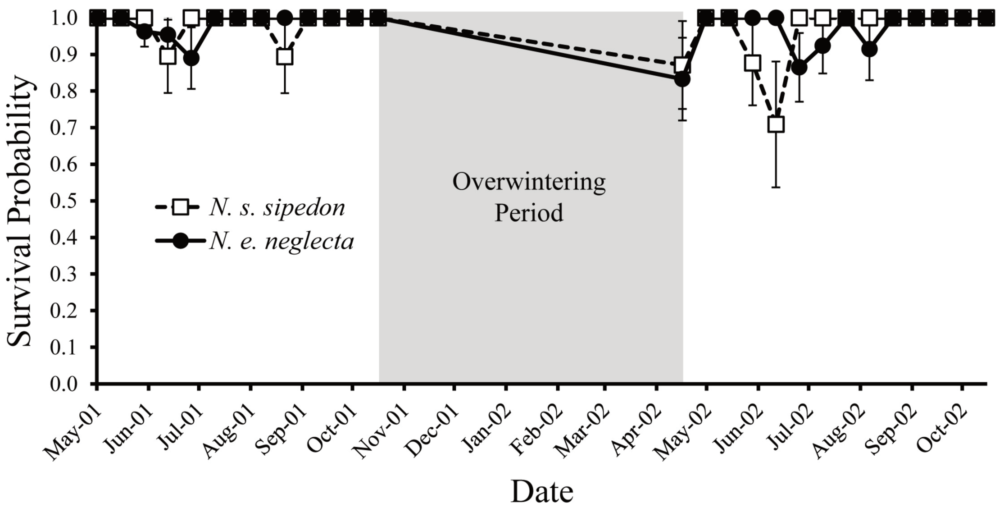

Figure 2. Survival probabilities over time for *Nerodia erythrogaster neglecta* and *N. sipedon sipedon*. Survival rates were determined at bi-weekly intervals except during overwintering when snake status could not be consistently confirmed, as they were below the surface for extended time periods. Values were derived from model *S* (species × time) SVL (see Table 2).

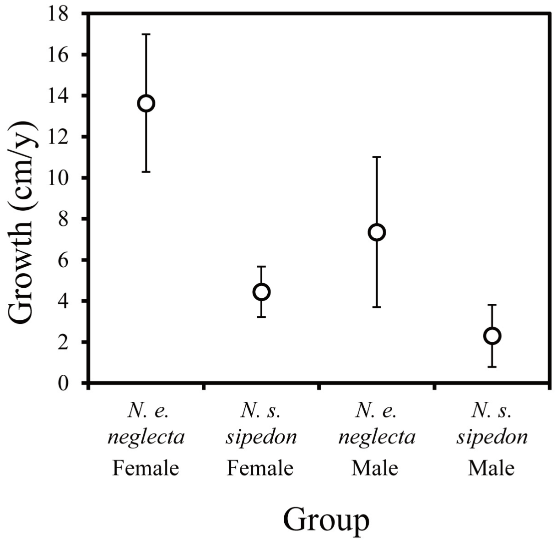

Figure 3. Annual growth rates for male and female *Nerodia erythrogaster neglecta* and *N. sipedon sipedon* studied by radiotelemetry.

However, the number of *N. e. neglecta* observed mating did not differ from *N. s. sipedon* for either sex ($\chi^2 < 2.39$, $P > 0.183$ for both tests).

Capture-mark-recapture.—We made 105 captures of 66 individual *N. e. neglecta*. The sex ratio of 1.3:1 (female:male) was not significantly different from 1:1 ($\chi^2 = 1.0$, df = 1, $P > 0.05$). *Nerodia. e. neglecta* ranged in SVL from 21.0–107.5 cm, and in mass from 9–1200 g (Fig. 4).

We recaptured and assessed growth in 15 female and 11 male *N. e. neglecta*. Intervals between captures ranged from 21–388 active season days. Growth rates were higher for females than for males over the entire size range of our sampled population (ANCOVA sex: $F_{1,23} = 8.6$, $P = 0.008$, SVL: $F_{1,23} = 28.8$, $P < 0.001$; Fig. 5). In the above analysis, the interaction between sex and body size was not significant ($P = 0.914$).

We captured 54 *N. s. sipedon*, with a sex ratio of 1.5:1 (female:male), which did not differ from 1:1 ($\chi^2 = 1.9$, df = 1, $P > 0.05$). *Nerodia. s. sipedon* ranged in SVL from 29.5–83.0 cm, and in mass from 15–515 g (Fig. 4). We did not assess growth rates for *N. s. sipedon* using capture-mark-recapture methods.

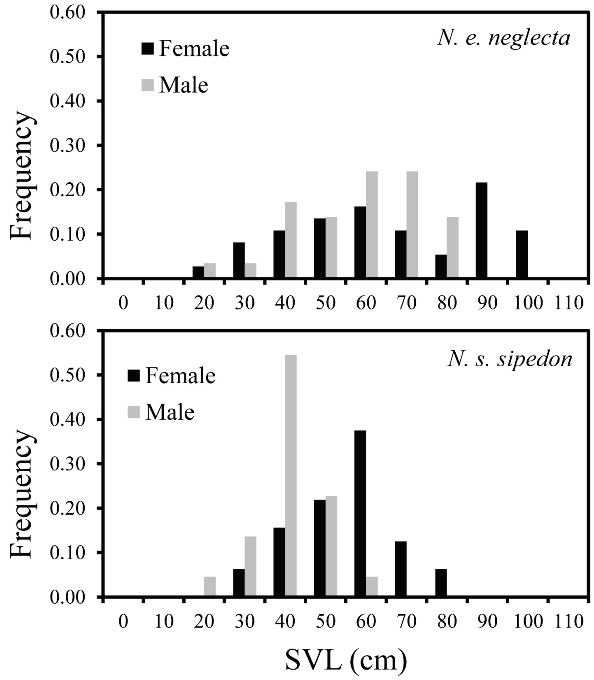

Figure 4. Size-frequency distributions for 29 male and 37 female *Nerodia erythrogaster neglecta* and 22 male and 32 female *N. sipedon sipedon*. Approximate size at maturity was assumed to be similar for both species, with males maturing at 43 cm SVL and females at 55 cm SVL.

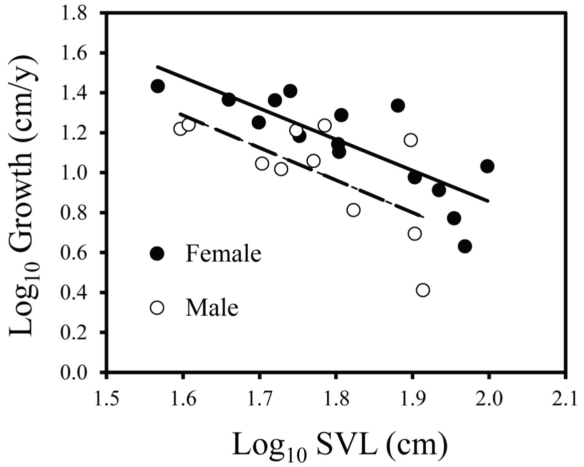

Figure 5. Relationship between annual growth rate and body size for male and female *Nerodia erythrogaster neglecta* as determined by capture-mark-recapture. Female growth rate = -1.56 SVL + 3.96 ($R^2 = 0.65$); male growth rate = -1.62 SVL + 3.88 ($R^2 = 0.45$).

Discussion

Our surveys indicate a declining *N. e. neglecta* population that is already of small size, perhaps numbering fewer than 100 adults (Attum et al. 2009). Based on relative abundance measures, the decline over the six-year study may be as much as 70%, though these measures do not take into account possible variation in detectability among sampling periods. Fluctuating environmental factors, such wetland drying, can influence aquatic snake abundance and activity in focal wetlands over time (Seigel et al. 1995; Willson et al. 2006). However, this was not likely the case during our surveys, which were conducted in spring, coinciding with flooded conditions at a time when *N. e. neglecta* concentrate activities in wetlands (Roe et al. 2003; 2004). Moreover, during the same surveys, *N. s. sipedon* sightings per unit effort remained relatively constant with the exception of 2002, when numbers increased. Because both species closely associate with shorelines and similar basking substrates within the wetland (Laurent and Kingsbury 2003) and are diurnally-active at our site (pers. obs.), behavioral differences between species are not likely to have biased our results. Thus, we suggest that the trends observed in *N. e. neglecta* most likely reflect actual population declines in our study system rather than temporal variation in watersnake detectability. This trend is concerning, as this *N. e. neglecta* population is thought to be the largest of the distinct northern population segment (Attum et al. 2009).

Given their imperiled status and demonstrated declines, we expected *N. e. neglecta* to have higher mortality rates than *N. s. sipedon*, but our models did not indicate clear differences in survival probability between species. The demographic models indicated the strongest differences in inter-specific survivorship, but contrary to expectations, survival estimates for *N. e. neglecta* males were considerably higher than male *N. s. sipedon*, while survival estimates for females of both species were relatively similar. However, we are cautious in interpreting these demographic comparisons given the low sample sizes. Nevertheless, our models do not indicate any particular vulnerability of *N. e. neglecta* to mortality, as adult annual survival rates for both species (0.63–0.67) were within the range of or higher than estimates of adult *Nerodia* sp. elsewhere (0.23–0.63; King 1986; Brown and Weatherhead 1999; Whiting et al. 2008; Roe et al. 2010).

On a finer temporal scale, determining whether peaks in adult mortality occur on a seasonal basis can highlight behaviors or times of year when individuals are most vulnerable to mortality, and thus help identify threatening processes. For instance, snakes may be particularly susceptible during reproductive behaviors and while overwintering, as the energy expenditure and risk of exposure to predators and unsuitable environmental conditions can result in higher mortality (Brown and Weatherhead 1997; Bonnet et al. 1999; Shine et al. 2001). In the presence of additional stressors that are already threatening populations, we might expect imperiled species to be even more vulnerable at these times. However, we found no such seasonal patterns in *N. e. neglecta* mortality, as survival was comparable between active and overwintering seasons, and no different than that of *N. s. sipedon* at these times. Based on evidence from carcasses and discarded transmitters, causes of mortality for *N. e. neglecta* included predation by snapping turtles, raptors, and mammals, and unidentified causes while overwintering, all of which are common sources or times of mortality in watersnakes (Brown and Weatherhead 1999; Roe et al. 2010). There was no indication of anthropogenic causes of mortality such as vehicular collisions, intentional killing, mowing, and/or other management practices. There were also no obvious symptoms of disease or parasites despite close observations for several days in the laboratory before and after transmitter implantation and frequent visual observations in the field.

Declines could also be explained by sublethal consequences with population-level implications, such as the inability to maintain positive energy balance for growth and maintenance of body condition (Congdon et al. 1982). For example, a decrease in body condition was associated with population declines of the snake *Lampropeltis getula* in South Carolina (Winne et al. 2007), and declines in *Thamnophis elegans* populations have been linked to reduced prey availability (Matthews et al. 2002). Conversely, higher individual growth rates in the watersnake *N. s. insularum* were associated with population increases, likely a result of increased prey abundance (King et al. 2006). If *N. e. neglecta* declines were attributable to food resource limitations, poor food quality, or excessive energy expenditure, we would expect these stressors to reduce individual growth rates relative to *N. s. sipedon* at the same site, or to *N. e. neglecta* elsewhere. However, this was not the case, as both female and male *N. e. neglecta* had growth rates three times higher than *N. s. sipedon* of the same sex, with rates equal to or higher than that of a more southerly *N. e. neglecta* population (U.S. Fish and Wildlife Service 2008). Significant growth was also evident in juvenile size classes for both sexes of *N. e. neglecta* in our capture-mark-recapture sampling, indicating growth rates in small snakes were not likely constrained by resource limitations either. Moreover, growth rates in *N. e. neglecta* were comparable to or higher than those of nearby *N. s. insularum* at a time when population size of the latter species was increasing (King et al. 2006). These relatively high growth rates are especially surprising considering that *N. e. neglecta* move farther distances and traverse larger areas than *N. s. sipedon* (Roe et al. 2004), activities that likely come with costs in energy expenditure that could lower growth rates if not balanced by sufficient energy intake (Secor and Nagy 1994).

Perhaps the most important fitness metric that could provide insight on *N. e. neglecta* declines is reproduction, but we were unable to collect direct information on reproductive success. One indirect measure of reproduction is the frequency with which individuals were observed mating (Brown and Weatherhead 1999). The lower densities of *N. e. neglecta* could reduce the chance of male and female encounters, but even though *N. e. neglecta* were observed mating less frequently than *N. s. sipedon*, the magnitude of difference was not significant. That we did not see clear differences between species in this reproductive metric is perhaps due to the rarity with which we observed mating behavior in any individual of either species. Another indicator of successful reproduction is the presence of juveniles in the population. *Nerodia* spp. in the region mature at approximately 43 cm SVL for males and 55 cm SVL for females (King et al. 1986; Brown and Weatherhead 1999). Assuming *N. e. neglecta* in our study population mature at similar sizes and ages, juveniles represented 14% and 27% of the males and females captured, respectively, which are comparable to values of 23% and 28% for male and female *N. s. sipedon*, indicating that recruitment had occurred in recent years. In the only other study of *N. e. neglecta* population demography, juveniles represented 10–32% of the sampled population over several years in a more southerly location (Lacki et al. 2005), which is comparable to that observed in *N. e. neglecta* in the current study. Clearly, more rigorous investigations of reproductive biology and direct measures of recruitment are needed to better interpret the observed *N. e. neglecta* population declines and their vulnerability to extinction (e.g., Reed and Shine 2000; Webb et al. 2002; Fitzgerald et al. 2004).

Disturbingly, the magnitude and timing of *N. e. neglecta* declines observed here is consistent with that of numerous other snake populations across the world (Reading et al. 2010), suggesting some global cause or suite of potentially interacting stressors operating synchronously in driving these precipitous declines. However, our examination of vital rates and population demographics did not reveal clear and consistent differences between syntopic species that could explain the decline of the *N. e. neglecta* population at our site. Nor can the observed declines in *N. e. neglecta* in our study be explained by a concomitant loss of preferred habitat, as the bulk of the population inhabits a protected wildlife management area that remained largely unchanged throughout the survey period. Thus, like many investigations of snake population declines, the proximate mechanisms behind the *N. e. neglecta* demise during our study remain unresolved (Winne et al. 2007; Reading et al. 2010). That is not to suggest that *N. e. neglecta* populations elsewhere or at this site in the past have not suffered reduced survival, growth, or reproduction in response to purported causative agents such as habitat fragmentation, the loss of shallow ephemeral wetlands, mining, road mortality, or declines in amphibian prey (Laurent and Kingsbury 2003; Roe et al. 2003, 2004; Lacki et al. 2005; Roe et al. 2006). It is possible that the study site, despite harboring one of the largest remnant populations, has been for some time of inadequate quality to sustain a viable population of *N. e. neglecta*, and that the declines we observed were part of an ongoing collapse. Indeed, relative abundance of *N. e. neglecta* (0.6–2.4 snakes/km) was lower in most years than those observed in a more southerly *N. e. neglecta* population (2.04–5.43 snakes/km; Lacki et al. 2005).

There are several methodological deficiencies that limit the above conclusions. First, the use of count data in surveys has the potential to identify negative temporal trends in the absence of real population fluctuations (Mazerolle et al. 2007). We therefore suggest additional surveys using formal occupancy modeling to re-assess the status of *N. e. neglecta*. A related limitation is that our surveys could not distinguish between population declines and temporary emigration from the study site. To address this shortcoming, we recommend that future surveys extend to a wider range of wetlands, both on and off reserve, and that surveys are augmented with capture-mark-recapture efforts designed to estimate emigration rates (e.g., robust design models; Dorcas and Willson 2009). In addition, our study represents only a snapshot into the long-term population dynamics of either species, necessitating more intensive monitoring to better elucidate mechanisms driving declines of *N. e. neglecta* and to separate natural population fluctuations from those driven by anthropogenic causes (Madsen and Shine 2001; Winne et al. 2007). Importantly, we were only able to collect vital rates and demographic data early in the survey period (2001–2003), leaving open the possibility that demographics and vital rates in *N. e. neglecta* may not have changed until later years in the survey period. However, some of the largest declines in *N. e. neglecta* abundance occurred between 2001 and 2003. Trends in vital rates and demographics do not explain the population trends during the same period, and certainly could not have been used to predict further declines in *N. e. neglecta* later in the surveys. Due to radiotransmitter constraints, small population size, and permit limitations, our sample sizes were small, especially when stratified into demographic groups. We were unable to examine survival rates in juveniles of either species, so any potential interspecific differences in mortality within this demographic group remain unresolved. Nonetheless, this study presents some of the first detailed estimates of population characteristics and vital rates in *N. e. neglecta*, serving as a useful benchmark for comparison in the future or at other sites, and providing critical information that can be used in population viability analyses to inform management. At a minimum, by eliminating some of the likely mechanisms of decline, we can perhaps proceed with more targeted approaches directed at examining other unexplored factors impacting *N. e. neglecta*.

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