



sloping grass-stabilized sandhills and loose sandy soils, and a typical mixed-grass prairie association consisting of gramma grasses (*Bouteloua* sp.), buffalo grass (*Buchloe* sp.), bluestem grass (*Andropogon* sp.), and sand sagebrush (*Artemisia filifolia*). West of

(Mackessy, 1998), and individually marked with PIT tags (Avid, Inc., Norco, CA). All snake manipulations were conducted with the approval of the UNC IACUC, protocols 9204.1 and 0501,

mean = 354 ± 174 ; N = 49); the adjusted activity period for this interval was 384 days.

Estimated Field Growth Rates.—The average growth rate per day (mm) for both female and male snakes during the active season decreased as snakes aged (females: adults = 0.067 ± 0.05 , N = 10; juveniles = 0.152 ± 0.24 , N = 11; YOY = 0.590 ± 0.21 , N = 5; males: adults = 0.098 ± 0.23 , N = 12; juveniles = 0.223 ± 0.13 , N = 8; YOY = 0.544 ± 0.24 , N = 3), though rates were generally higher in males (Fig. 5); t-tests indicated that these trends were not statistically different between the sexes (neonates: P = 0.403; juveniles: P = 0.212; adults: P = 0.187). Linear regression analysis indicated strong negative correlations (P < 0.001) between percent increase in length (mm) and growth rate (mm per day) versus initial SVL for both male and female snakes (Fig. 6).

Population Estimate.—During 2005, 2006, and 2007, 672 individuals were PIT-tagged to identify individuals and to estimate population size. Using the Schnabel (1938) method, the estimated Desert Massasauga population (Table 2, 0.7 snake/ha) at our study site (4,860 ha) was 3,563 (95% CI: 2784, 4949). Regressing the proportion of marked snakes against the number of those previously marked (a test of model assumption violations; Krebs, 2009) produced a linear relationship ($R^2 = 0.94$; P < 0.001).

Activity and Movement Patterns.—Based on road and vegetation surveys, drift fence/funnel trap surveys, and radiotelemetry

surveys, Desert Massasaugas are active in this Colorado population from approximately mid-April until late October. Desert Massasaugas within this population make long-distance seasonal movements (spring/fall mill ategiM686.9(m)-4.3.9(f0 -1.-7.2)

2006, three females gave birth to two to four young in middle to

Desert Massasaugas PIT-tagged in four field seasons. No other populations in the known distribution show densities this high (estimated at approximately 3,500 in 4,800 ha). During peak migration periods in spring and fall, we commonly encountered upwards of 20 snakes during a single pass of the 3 km road that divides summer foraging habitat and winter hibernacula. Neonate and juvenile snakes grow rapidly during their second year but are typically not captured until fall, leading to the apparent “missing size classes” in Figure 3. Analysis of field growth rates and size class frequency distributions from recapture data showed that the average snake encountered was approximately 3 yr old; 4-yr-old snakes were also frequently encountered, but less than 4% were considered to be \pm 5 yr. The lack of snakes greater than the fourth year size class, coupled with a maximum recapture interval of 2 yr and a recapture rate during the 2005–2007 active seasons of 6.5%,

a-1.8(s)-859.2io54.9ure10.4(a28.1(to).8(e10.4r)66.9ns)-91.(C)14.1(o54.9l)44.1(o54.9r)5.6(a-1.8d)64.6oa

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high, as evidenced by a large number of neonate captures during fall migration.

The high densities of Desert Massasaugas and at least 15 other species of reptiles and amphibians at the study site indicate that, numerous conditions (habitat and microhabitat availability and quality, suitable hibernacula, abundance of appropriate prey, and lack of important anthropogenic disturbance), are ideal for a diverse north temperate herpetofauna. The current landowners have been practicing rotational grazing of a modest herd of cattle on the site for many years, and this practice has likely promoted the continued persistence of many species, including Desert Massasaugas. However, in recent years, the habitat quality of the study site has diminished attributable to extended drought conditions that appear to favor an increase in invasive weed species such as Russian Thistle (*Salsola* sp.), Kochia (*Kochia scoparia*), Sandbur (*Cenchrus longis-*

- . 2005. Desert massasauga rattlesnake (*Sistrurus catenatus edwardsii*): a technical conservation assessment. USDA Forest Service. Available from: <http://www.fs.fed.us/r2/projects/scp/assessments/massasauga.pdf>. Accessed 15 May 2015.
- OLSSON, M., T. MADSEN, AND R. SHINE. 1997. Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proceedings of the Royal Society of London B Biological Sciences* 264:455–459.
- PARKER, W. S., AND M. V. PLUMMER. 1987. Population ecology. Pp. 478–513 in R. A. Seigel and J. T. Collins (eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Company, USA.
- PATTEN, T. J. 2006. Spatial Ecology and Natural History of the Western Massasauga Rattlesnake (*Sistrurus catenatus tergeminus*) in South-eastern Nebraska. Unpubl. master's thesis, University of Nebraska, Omaha, USA.
- PIKE, D. A., L. PIZZATTO, B. A. PIKE, AND R. SHINE. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* 89:607–611.
- REINERT, H. K., AND W. R. KODRICH. 1982. Movements and habitat utilization by the massasauga, *Sistrurus catenatus catenatus*. *Journal of Herpetology* 16:162–171.
- REINERT, H. K., AND R. R. RUPERT JR. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. *Journal of Herpetology* 33:45–61.
- REINERT, H. K., AND R. T. ZAPPALORTI. 1988. Field observations of the association of adult and neonatal timber rattlesnakes, *Crotalus horridus*, with possible evidence for conspecific trailing. *Copeia* 1988:1057–1059.
- RIEDLE, J. D. 2014. Demography of an urban population of ring-necked snakes (*Diadophis punctatus*) in Missouri. *Herpetological Conservation and Biology* 9:278–284.
- ROSEN, P. C., AND S. R. GOLDBERG. 2002. Female reproduction in the western diamond-backed rattlesnake, *Crotalus atrox* (Serpentes, Viperidae) from Arizona. *Texas Journal of Science* 54:347–356.
- SCHNABEL, Z. E. 1938. The estimation of the total fish population of a lake. *American Mathematics Monthly* 45:348–352.
- SCHUETT, G., D. L. CLARK, AND F. KRAUS. 1984. Feeding mimicry in the rattlesnake *Sistrurus catenatus*, with comments on the evolution of the rattle. *Animal Behavior* 32:625–626.
- SEIGEL, R. A. 1986. Ecology and conservation of an endangered rattlesnake, *Sistrurus catenatus*, in Missouri, USA *Biological Conservation* 35:333–346.
- SEIGEL, R. A., AND J. T. COLLINS. 1993. *Snakes: Ecology and Behavior*. McGraw-Hill Book Company, USA.
- SEIGEL, R. A., J. W. GIBBONS, AND T. K. LYNCH. 1995. Temporal changes in reptile populations: effects of a severe drought on aquatic snakes.