Journal of Herpetology, Vol. 50, No. 4, 594–603, 2016

Desert Massasauga Rattlesnakes (*Sistrurus catenatus edwardsii*) in Southeastern Colorado: Life History, Reproduction, and Communal Hibernation

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ABSTRACT.—**We studied Desert Massasauga Rattlesnakes (*Sistrurus catenatus edwardsii*) in southeastern Colorado in 1998 and 2005–2007. Mark–recapture data for 770 snakes indicated a population size of >3,500 snakes in an area of approximately 4,800 ha. Field growth rates and size class frequency distributions showed that average snake age was 3 yr; 4 yr old snakes were frequently encountered, but less than 4% were 5 yr or older, suggesting low survivorship beyond this age. Conversely, initial growth was rapid; snakes grew an average of 0.57 mm/day in their first full year. Desert Massasaugas mated in fall and spring, producing 2–7 (mean 3.3) young in late August to early September, and reproduction appeared to be biennial. Desert Massasaugas showed maternal attendance for at least 5 days postparturition, and neonate dispersal corresponded with the first shed. Radioed Desert Massasaugas (*N* = 15) used rodent burrows as hibernacula, and within 50 m of Desert Massasauga hibernacula, eight snake, five anuran, and two turtle species use the same area for hibernation. Low prey density at the hibernaculum indicates that stable hibernation conditions are the primary resource attracting a diverse assemblage of species to this area. The hibernaculum area serves as a critically important winter refuge for numerous species and supports the largest known population of Desert Massasaugas. This population is considered stable at present; however, because of rapidly changing climatic conditions, habitat loss and degradation, anthropogenic disturbance, and shifts in prey abundance, it may become threatened in the near future, and continued monitoring is warranted.**

Snakes are highly specialized, secretive vertebrates, and many aspects of their ecology and population biology are poorly understood (Henderson and Hoevers, 1977; Ford, 2002; Clark et al., 2014). Some may be locally abundant and make up a substantial portion of biomass in areas where they occur (Godley, 1980; Shine and Madsen, 1997; Wilson and Dorcas, 2004, Riedle, 2014). For these ectothermic animals, basic life-history characteristics such as growth and reproduction are strongly influenced by stochastic events, such as prey and surface water availability during or preceding the period in which sampling occurs (Parker and Plummer, 1987; Seigel et al., 1995). Additionally, there are numerous difficulties associated with conducting detailed life-history studies for snake populations. Snakes are difficult to observe in the field, making behavioral studies challenging, and apparent low-density estimations may result from cryptic patterns and secretive habits. Snakes are prone to long periods of inactivity and typically feed infrequently, and these habits greatly hamper attempts to obtain sufficient sample sizes for studies on foraging and community ecology (Henderson and Hoevers, 1977; Turner, 1977; Parker and Plummer, 1987; Vitt, 1987). As a result, snakes are often difficult to capture repeatedly (Ford, 2002), exacerbating the difficulty in obtaining basic life-history data. Some snakes living in cold climates, that often den communally, have life-history habits that lend themselves well to ecological inquiries and several species have been the subject of intensive studies (e.g., *Crotalus* [*viridis*] *oreganus*, Diller and Wallace, 1996; *Crotalus horridus*, Brown, 1993; *Sistrurus catenatus edwardsii*, Wastell and Mackessy, 2011; *Thamnophis sirtalis*, Larsen et al., 1993; *Nerodia sipedon*, Brown and Weatherhead, 1999).

Currently, there are three recognized subspecies of *Sistrurus catenatus*: the Eastern Massasaugas, *Sistrurus catenatus catenatus*, that inhabit the wet prairies and swamps from western New York and southeastern to Ontario to eastern Iowa and eastern Missouri; the Western Massasaugas, *Sistrurus catenatus tergeminus*, found on the plains and prairies from southwestern Iowa and northwestern Missouri south to central Texas; and the Desert Massasaugas, *S. c. edwardsii*, that inhabit arid-xeric grasslands from western Texas to southeastern Arizona and occur in disjunct populations in Colorado and the Mexican states of Coahuila and Nuevo Leon (Conant and Collins, 1991; Hobert, 1997; Fig. 1). In Colorado, Desert Massasaugas have been designated as imperiled by the Colorado Natural Heritage Program (CNHP) and are considered a Species of Special Concern by Colorado Parks and Wildlife (Mackessy, 1998, 2005; CNHP, 1999). In 2012, the United States Fish and Wildlife Service (USFWS) announced a 90-day finding on a petition to list Desert Massasauga rattlesnakes as endangered or threatened under the Endangered Species Act of 1973 and to designate critical habitat. Based on their review, the USFWS found that the petition presents substantial scientific or commercial information indicating that listing Desert Massasauga rattlesnakes may be warranted. Accordingly, the USFWS will initiate a review of the status of this subspecies to determine whether listing is warranted.

Two previous studies reviewed basic life-history parameters for Desert Massasaugas for all of southeastern Colorado (Hobert et al., 2004; Mackessy, 2005); however, because this species occurs over a large area in Colorado, detailed population demographics were not obtained. For the present study, efforts were focused on a large population located in southeastern Colorado that has been studied by our lab since 1995; this population was also the subject of a study on spatial ecology conducted in 1998 and in 2005–2006 (Wastell and Mackessy, 2011). The objective of this study was to determine life-history characteristics of this population of Desert Massasaugas, including population size, size/age class distribution, growth rates and sex ratio, reproduction, and hibernation habits.

MATERIALS AND METHODS

Study Site and Habitat Description.—The study area comprises approximately 4,860 ha on a private ranch in Lincoln County, Colorado, USA, divided along a north/south axis by a dirt road (Fig. 2). East of the road, the area is characterized by gently

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DOI: 10.1670/15-084

FIG. 1. Range of Massasauga Rattlesnakes (*Sistrurus catenatus*) in North America. The study site in Colorado (*) is at the northern limit of the distribution of Desert Massasaugas. Adapted from Mackessy (2005).

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 the road, the area slopes downward to the drainage of the site (an unnamed intermittent stream) that roughly parallels the dirt road in an N–NW to S–SE direction. The hibernaculum area is located ~100 m east of the drainage, and immediately east and west of this drainage, the soil is loamy/dense (referred to as hardpan), with vegetation typical of short-grass prairie habitat and consisting of gramma grasses, buffalo grass, and prickly pear (*Opuntia* sp.). Habitat was characterized using a combination of Colorado Vegetation Classification Project maps (supplied by Colorado Parks and Wildlife, CPW), Department of Soil Conservation maps (USDA, 1965; USDI, 1967), and field descriptions of microhabitat used by individual Desert Massasaugas that were obtained during a radiotelemetry study (Wastell and Mackessy, 2011). The study site shows typical mid-continental climatic conditions, with warm–hot summers and late monsoonal rainfall and cold (well below 0°C) winters with sparse-low snowfall (Table 1; data from Karval, CO).

Population Demographics: Snake Sampling, Measurements, and Natural History Observations.—We used a combination of road and vegetation surveys, drift fence/funnel traps ($N = 6$; 33 m fences, 0.4 m tall), and radiotelemetry surveys for massasaugas ($N = 36$) at the study site in spring through fall of 1998 and 2005–2007 (surgically implanted radios, 1.6–2.5 g; see Wastell and Mackessy, 2011). Because researchers were present continuously at the site during these years, the additional data presented here were gathered concurrently with the radiotelemetry/spatial ecology study (Wastell and Mackessy, 2011), both opportunistically and anecdotally. The published study contains detailed methodologies regarding radio-implantation and telemetry and, thus, is not repeated here.

At each snake encounter, locality data (UTM coordinates; NAD 83) were taken with a Trimble GPS unit. All massasaugas encountered were collected using snake hooks and brought to the University of Northern Colorado (UNC) Animal Resource Facility for handling. Measurements were recorded by hand on non-anesthetized snakes and included mass (g), snout-to-vent length (SVL), tail length, sex, rattle segment number (basal + x), and age class categorization (neonate, juvenile, or adult). Sex was determined by the larger values of SVL to tail length ratios of males, and this was verified in approximately 200 snakes using standard hemipenial probing techniques. Because snake lengths obtained on non-anesthetized snakes can be variable (D. Cundall, pers. com.); snakes were stretched gently, allowed to relax, and then extended again to obtain consistent estimates of length (±5 mm). Snakes were also extracted of venom

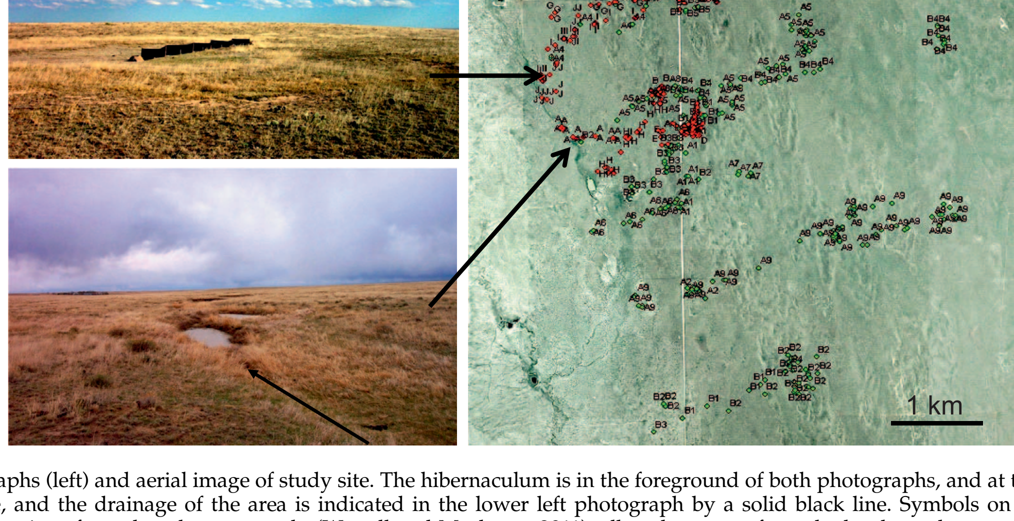

FIG. 2. Photographs (left) and aerial image of study site. The hibernaculum is in the foreground of both photographs, and at the tips of the arrows in the aerial image, and the drainage of the area is indicated in the lower left photograph by a solid black line. Symbols on the aerial image are individual snake locations from the telemetry study (Wastell and Mackessy, 2011); all snakes move from the hardpan shortgrass habitat (left side of image) to forage during summer months in the sandhills habitat (right side; primarily east of road).

TABLE 1. Climate variables in Karval, CO (1981–2010 averages).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Average high (°C)	7.2	8.3	12.8	17.8	22.2	27.8	31.7	30	26.1	19.4	12.2	6.7
Average low (°C)	−8.9	−7.8	−3.3	0.5	6.1	11.1	14.4	13.9	8.3	1.7	−4.4	−8.9
Average precipitation (mm)	7.1	7.9	21.1	32.0	54.1	51.1	68.1	59.9	23.1	23.9	9.9	7.9
Average snowfall (mm)	101.6	76.2	127	76.2	0	0	0	0	0	25.4	76.2	127

(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, and in accordance with established guidelines (American Society of Ichthyologists and Herpetologists/Society for the Study of Amphibians and Reptiles).

Surveys were conducted through the entire active season, from mid-April through late October. A full-time graduate student (ARW) was on site during the active season conducting daily road surveys, checking and maintaining drift fence/funnel traps, and obtaining daily locations (average days tracked for each snake during active season was 143) of radioed snakes throughout the study site ($N = 12$). Surveys were generally conducted at the time of day when snakes were most likely to show surface activity (average 26.4°C; Wastell and Mackessy, 2011), and the time of day varied seasonally. In total, 36 radioed snakes were tracked during the telemetry portion of the study, but because of radio failures, only 12 were tracked for an entire season. Seasonal migration occurs in Desert Massasaugas from approximately 15 April to 15 May and 15 August to 15 October (Wastell and Mackessy, 2011), and large numbers of snakes cross a dirt road to and from the hibernaculum. Road survey efforts were increased at these times to maximize capture rate, because in spite of intensive field surveys, Desert Massasaugas were rarely encountered in the field. During this fieldwork, various natural history observations were also recorded, including predation events, courtship/mating, male–male combat, and occurrence of other reptile and amphibian species at the hibernaculum.

An AVID MiniTracker PIT-tag reader (Avid Identification Systems, Inc. Norco, California, USA) was used to scan all snakes encountered. Recapture data were analyzed in Microsoft Excel and Sigma Plot. Growth rate was determined by analyzing the following parameters: interval between capture dates, difference in SVL from initial capture to recapture, and difference in mass from initial capture to recapture. The inactive season, approximately 15 October through 15 April (180 days), was subtracted from the capture interval when appropriate with the assumption that snakes do not add significant body mass or length during hibernation. Growth rate data were used in confirming age/size class definitions within the study population. Population size was estimated using the Lincoln–Peterson index model of Schnabel (1938). Attempts to use the program MARK were unreliable and are not reported here. Unlike previous reports (e.g., Hobert et al., 2004), we recorded measurements from only live snakes.

Reproduction.—In 2005 ($N = 3$) and 2006 ($N = 3$), we tracked six gravid female Desert Massasugas from spring migration through birthing and attendance of neonates; movement patterns of these females were previously reported (Wastell and Mackessy, 2011). Starting in early August, radioed gravid females were located at least twice per day to increase the likelihood of observations of neonates. Following parturition, we collected data on: clutch size, position of neonates and female at birthing site, duration of neonatal attendance by the female, and the duration that neonates remained at birthing sites. Females and neonates were not disturbed or collected to observe any natural behaviors in the field. Additional field observations on aspects of reproduction were obtained during radiotelemetry of nongravid snakes and during habitat surveys. Two gravid females (one in 1998, one in 2005) were held in captivity through parturition to obtain morphological information for neonates. An approximation of the cost of reproductive effort, in terms of lowered body mass assimilation, was evaluated by comparing mass at capture of postparturient and nonreproductive adult female Desert Massasaugas. Adult female snakes ($N = 135$) were evaluated via palpation as postpartum ($N = 31$) or non-postpartum ($N = 104$), and mass and SVL were recorded. Data were analyzed using ANCOVA with reproductive status (postpartum, non-postpartum) as the independent variable, mass as the dependent variable, and SVL as the covariate. Levene's test of equality of error variance showed nonsignificant results, indicating that there is equal variance between the two groups. For all tests, $\alpha = 0.05$ and descriptive statistics are expressed as mean + SD.

Hibernaculum Surveys.—The hibernaculum area (Fig. 2) was surveyed for all species of amphibians and reptiles using visual encounter surveys, drift fence/funnel traps, and auditory surveys (amphibians). Drift fence traps (two 33 m fences, 0.4 m tall) were installed prior to egress (first week of April) and ingress (early September). Funnel traps (25 × 100 cm) were placed at the ends of drift fences, covered with shade boards, and checked daily.

RESULTS

Population Demographics.—We captured 770 Desert Massasaugas (374M : 348F : 48 unknown) and categorized them into 10-mm size classes (including 36 used in the previously reported telemetry study; Fig. 3). The small number of snakes in the size classes 240–290 mm resulted from time-biased sampling, which was not clear until recapture data were analyzed (see below). Based on recapture data for 49 snakes captured during 2005–2007, growth rates obtained from individual snakes, morphological data for 770 snakes, and previous analyses (Mackessy, 2005), age/size classes were defined as follows: neonate and young of year (YOY): SVL = 160–219 mm; second year: SVL = 220–359 mm; third year: SVL = 360–399 mm; fourth year: SVL = 400–429 mm; fifth year: SVL = 430–459 mm; sixth year: SVL: 460–475 mm; and seventh plus year: SVL = 480+ mm (Figs. 3, 4). Of the 770 snakes captured, 341 were adults (SVL $\geq$350 mm), 251 were juveniles (SVL = 230–340 mm), and 178 were neonates and YOY (SVL $\leq$220). The mean SVL (± SD) of adult males (394 ± 29 mm) was significantly greater than the average SVL (± SD) of adult females (380 ± 23 mm) (*t*-test; $t_{340} = 4.70$, $P < 0.001$). The male : female sex ratio for the entire study population ($N = 722$) is 1.07, and the male : female sex ratio for only adults within the study population ($N = 341$) is 1.09. The longest duration for recapture of a PIT-tagged snake was 744 calendar days (minimum = 30;

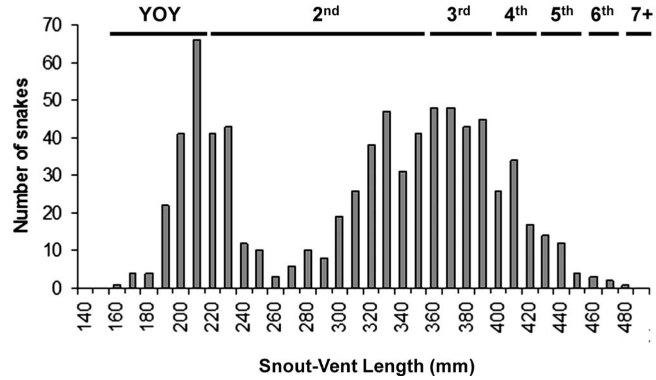

FIG. 3. Size distribution of Desert Massasaugas captured at the study site, 1998 and 2005–2007 ($N = 770$). Bars and numbers above histograms indicate age class as defined in Results. YOY, young of year.

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 migration) to and from hibernacula (see Wastell and Mackessy, 2011). The earliest date a snake was found was 10 April 2006, when two snakes were observed basking near the hibernaculum; most snakes were observed moving during spring migration, from mid-April through mid-May. Following fall migration (early September through early October), Desert Massasaugas had a brief ingress, but snakes were observed basking near hibernacula as late as 12 November (one radioed snake, 1998). We found snakes most commonly in April (128), August (152), September (181), and October (145) and least commonly encountered in June and July (Fig. 7). These findings are also similar to those reported by Hobert et al. (2004) for Desert Massasaugas in all of Colorado.

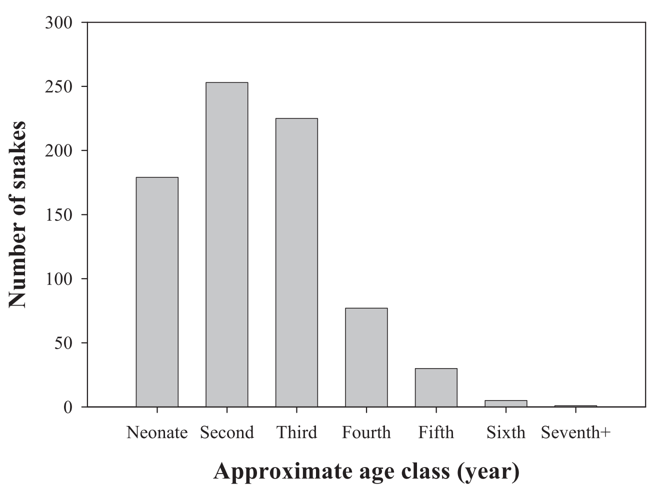

FIG. 4. Approximate age class frequency of Desert Massasaugas captured at the study site, 1998 and 2005–2007 ($N = 770$). Snakes older than four years were rarely encountered.

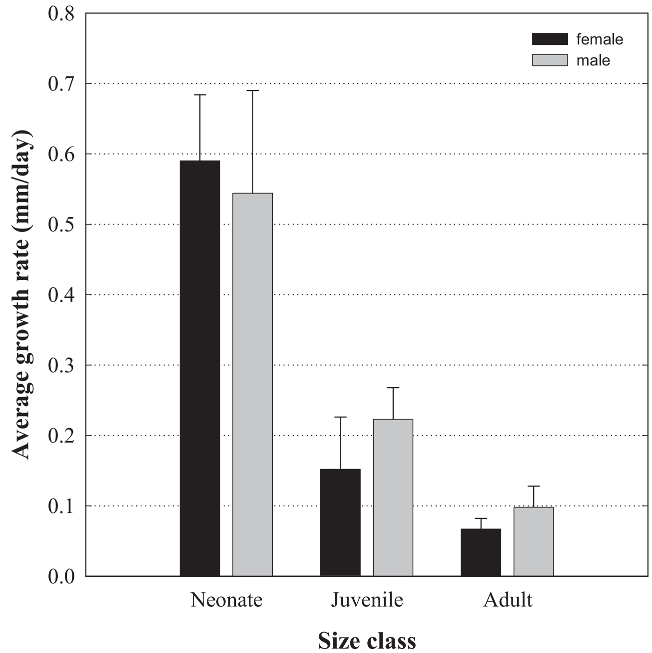

FIG. 5. Average daily growth rates of three size classes of Desert Massasaugas (±1 SE, $N = 49$). Although juvenile and adult male snakes tend to show higher growth rates than females, these differences are not statistically different.

Reproduction.—In 2005 and 2006, six radioed gravid female Desert Massasaugas were tracked from spring migration through birthing and attendance of neonates at rodent burrows in the sand sagebrush habitat. In 2005, three females gave birth to three to five young in late August and early September (five neonates born on 20 August: four on 22 August; three on 5 September). In

TABLE 2. Population estimate from mark-recapture data in 2005–2007 using the Schnabel method.

Sampling period	Captured (C)	Recaptures (R)	Unmarked (C-R)	Cumulative marked (M)	C × M
Spring 2005	30	0	30	0	0
Fall 2005	171	1	170	30	5,130
Spring 2006	77	7	70	200	15,400
Fall 2006	165	8	157	270	44,550
Spring 2007	97	12	85	427	41,419
Fall 2007	133	21	112	512	68,096
		49			174,595

N = 3,563 (95% CI: 2784, 4949).

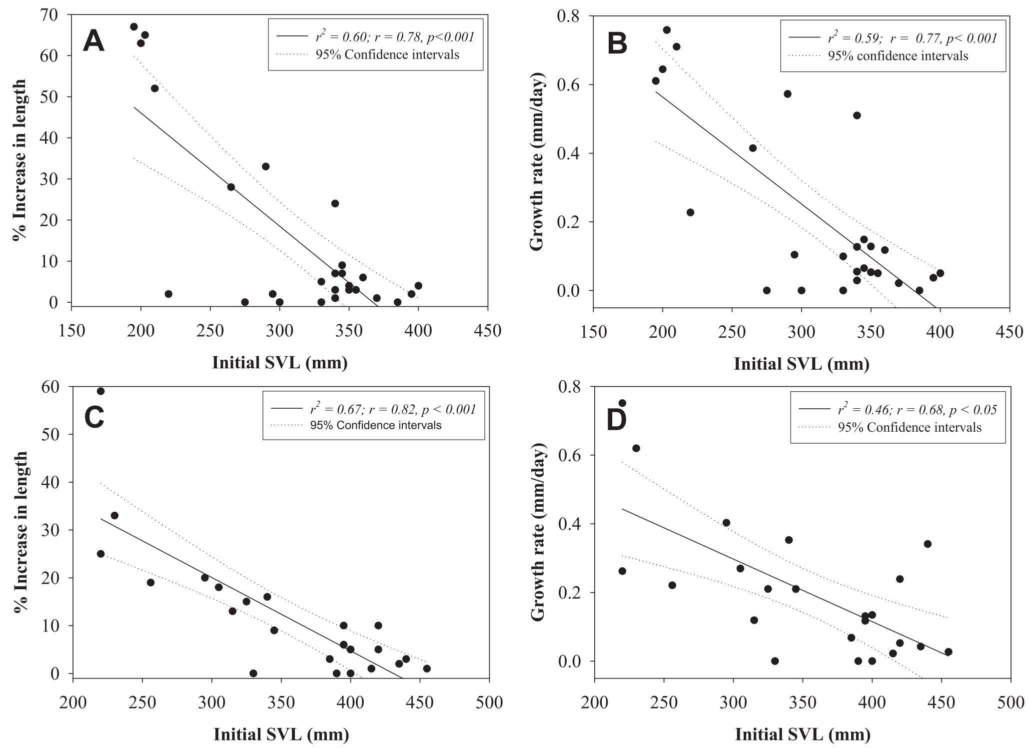

FIG. 6. Field growth rate estimates for female and male Desert Massasaugas in Colorado. (A) Percent increase in length of females as a function of initial capture length ($N = 26$). (B) Growth rate of females as a function of initial capture length ($N = 26$). (C) Percent increase in length of males as a function of initial capture length ($N = 23$). (D) Growth rate of males as a function of initial capture length ($N = 23$). All plots are based upon recapture data obtained for snakes in 2005–2007. SVL, snout–vent length.

2006, three females gave birth to two to four young in middle to late August (two offspring on 14 August: two on 16 August: four on 30 August). The average clutch size for Desert Massasaugas born in the field at the study site was 3.3 ± 1.2 ($N = 6$; Table 3). Neither the females nor the offspring born in the field were collected or disturbed, and no morphological data were obtained for these neonates. Because all females known to give birth in the field contained radiotransmitters, which could affect development in these small rattlesnakes, and because of small sample size, examining clutch size as a function of SVL was not feasible. Captive-born neonates ($N = 9$) averaged 155 mm SVL and 3.97 g (Mackessy, 2005).

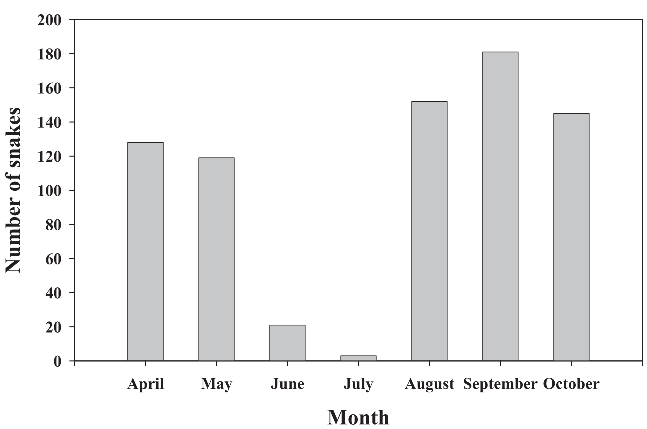

FIG. 7. Number of Desert Massasaugas encounters per month for 2005–2007 ($N = 770$). Note that June and July are underrepresented because snakes are in summer foraging areas in the sand hills, are highly cryptic, and are rarely encountered.

For 3 wks prior to giving birth, females became highly stationary, basking near (or just inside) the same rodent burrow and appearing to take up "long-term residency" at birthing sites (Fig. 8A). All birthing sites were small rodent burrows in the mixed grass/sand sagebrush habitat, and they all had exposed sandy sites that were used for basking. Neonates were frequently observed basking at or just inside the burrow entrance, near or on top of the female (Fig. 8B). Females left the birth site five to seven days ($N = 6$; mean = 5.7 ± 0.8) after giving birth, suggesting that female attendance occurs in Desert Massasaugas. One of the females was observed in copulation within 24 h after leaving the birth site. The neonates remained at the birthing site until their first shed (~6 days) and then dispersed, heading generally westward. Female dispersal from the birth site concurred with neonate ecdysis and dispersal from the birth site. A large number of neonates ($N = 110$) and adults ($N = 168$) were encountered individually crossing the county road (heading west toward hibernacula) in mid-August through early October.

The potential cost of reproductive effort, in terms of lowered body mass assimilation, was evaluated by comparing mass at capture in fall of postparturient and nonreproductive adult female Desert Massasaugas. Average body mass of nonreproductive females was 35.4 ± 0.46 g ($N = 104$), whereas postpartum females were 30.7 ± 0.85 g ($N = 31$). Postparturient females generally showed an obvious decreased muscle tone and mass of the posterior third of the body, and they were significantly lighter than nonreproductive females ($P = 0.001$).

On 27 April 2006, two adult male Desert Massasaugas were observed in male–male combat, a behavior in the wild previously undocumented for this species. This behavior was observed for ~5 min, and not until approached by the observer

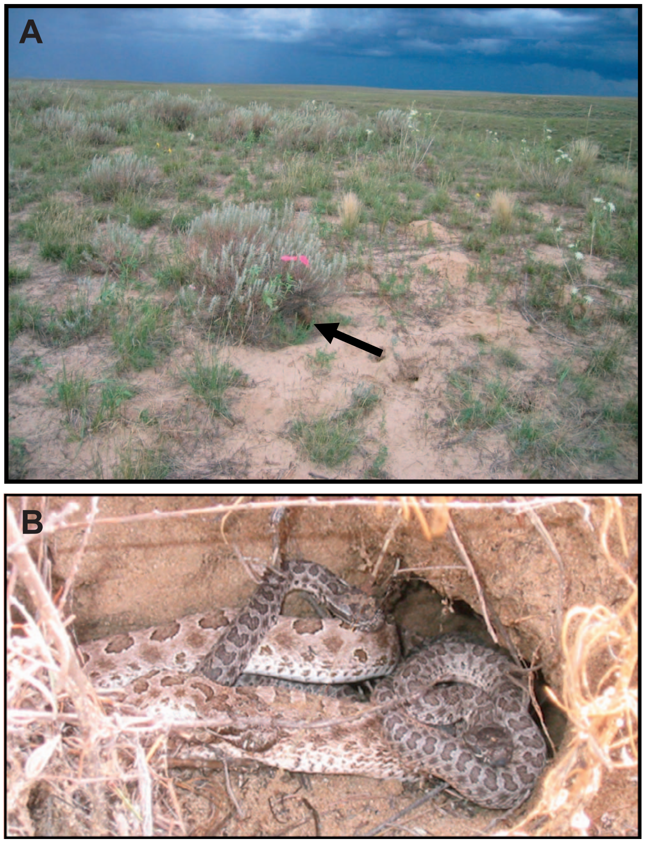

FIG. 8. (A) Birth site for snake 148.396; the black arrow indicates the opening to the rodent burrow used as a retreat. The opening faces west/southwest. (B) Female Desert Massasauga (snake 148.396) showing maternal attendance of neonates. Pre-ecdysis neonates were frequently observed basking on or near their mother; two are visible.

(within 1 m) did the snakes cease combat. The two snakes held the anterior ends of their bodies approximately 40–50% off of the substrate while swaying back and forth. Each snake appeared to be attempting to reach a higher vertical stature than the other, while repeatedly hooking one another as if to throw the opponent off balance. Both snakes were subsequently collected for processing and radio-implantation.

Mating and courtship were observed in both the spring and the fall. We found two breeding pairs courting and copulating in the spring: one pair at the spring emergence site in late April, and the other during spring migration in early May. We found two breeding pairs courting and copulating in early September in summer foraging grounds just before beginning fall ingress movements.

Predation.—Two radioed snakes (one male, one non-gravid female) were likely predated by Long-Tailed Weasels, *Mustela frenata*. When attempting to obtain a daily location of the nongravid female in an area where several weasels were recently and repeatedly captured in funnel traps, the erratic nature of the radio signal became evident (the intensity of which traveled rapidly back and forth over a 20–30 m distance, underground, and there was no visually apparent surface activity) and likely was due to predation by a Long-Tailed Weasel.

Hibernation.—Based on movement data of radioed massasaugas, as well as on field observations (drift fence traps, visual encounter surveys, road surveys), snakes made long-distance movements in the spring (mean 1.89 km; range 1.02–3.46 km) from the hibernaculum to summer foraging areas (Wastell and Mackessy, 2011). Snakes returned to the hibernaculum area in fall. Radioed Desert Massasaugas ($N = 15$) used rodent burrows as hibernaculum sites, and they appeared to occupy them individually. Average distance between spring emergence site and fall ingress sites for radioed snakes (Wastell and Mackessy, 2011), a measure of hibernation site fidelity (Patten, 2006), was 126.2 ± 94.3 m ($N = 6$); no radioed snake was observed to enter the same burrow in fall from which it had emerged that spring. However, within 50 m of individual massasauga hibernacula, numerous large "sinkhole" openings occur, and multiple species were observed entering these sites in the fall, exiting in the spring and basking in the immediate vicinity shortly before ingress and following egress. Prairie Rattlesnakes (*Crotalus viridis viridis*) were most commonly observed, and Glossy Snakes (*Arizona elegans*), Racers (*Coluber constrictor*), Milksnakes (*Lampropeltis triangulum*), Bullsnakes (*Pituophis catenifer*), Coachwhips (*Masticophis flagellum*), and Desert Massasaugas (*S. c. edwardsii*) were also found in the same holes and in the immediate vicinity (Table 4). The shortgrass prairie and adjacent drainage (linear distance from sinkholes to stream <100 m) also contained high densities of Plains Garter Snakes (*Thamnophis radix*), Ornate Box Turtles (*Terrapene ornata*), Plains Spadefoot Toads (*Spea bombifrons*), Woodhouse Toads (*Anaxyrus woodhousii*), Great Plains Toads (*Anaxyrus cognatus*), Plains Leopard Frogs (*Lithobates blairi*), and Chorus Frogs (*Pseudacris maculata*) (Table 4).

TABLE 3. Reproduction data for Desert Massasaugas in southeastern Colorado.

Snake ID	Parturition date	Clutch size	No. days maternal attendance
149.661	8/20/2005	5	6
148.396	8/22/2005	4	5
148.452	9/5/2005	3	6
149.671	8/14/2006	2	5
149.371	8/16/2006	2	5
149.731	8/30/2006	4	7
mean	8/23	3.3	5.7

DISCUSSION

This study represents the largest, most comprehensive data set for the Desert Massasauga Rattlesnakes to date, with 770

TABLE 4. Reptile and amphibian species encountered at hibernaculum area during 2005–2006.

	No. encounters
Snakes	
Sistrurus catenatus edwardsii	90
Crotalus viridis viridis	152
Coluber constrictor	15
Masticophis flagellum	10
Thamnophis radix	20
Pituophis catenifer	7
Lampropeltis triangulum	1
Arizona elegans	1
Amphibians	
Spea bombifrons	4
Anaxyrus woodhousii	13
Anaxyrus cognatus	31
Lithobates blairi	21
Pseudacris maculata	10
Turtles	
Terrapene ornata	15
Kinosternon flavescens	1

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 $\geq$ 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%, suggests that overall survivorship is low for Desert Massasaugas in southeastern Colorado. This population dynamic contrasts strongly with a Prairie Rattlesnake den site in northeastern Colorado, where recapture rates approach 30% annually, and snakes have been recaptured for up to 12 yr (unpubl. obs., SPM). Because Desert Massasaugas have survived in captivity to at least 20 yr of age (unpubl. obs., SPM), predation rates and other causes of mortality are assumed to be quite high. Conversely, initial growth was quite rapid; snakes grew an average of 0.57 mm/day in their first full year, and snakes are reproductive by their third year. In addition to predation, persecution by humans (intentional killing, road mortality), and/or disease may be important factors greatly limiting the survivorship potential in the wild for these small rattlesnakes (Mackessy, 2005). Emigration may possibly affect population estimates, but because this area is surrounded by much more degraded shortgrass/mixed grass habitat, and because of near-unique habitat features favoring massasauga abundance on this site, emigration is unlikely an important factor at present. In addition, the strong linear relationship between marked and previously marked snakes suggest the violations of the population model assumptions were small.

The average SVL of adult males was significantly greater than the average SVL of adult females. This size dimorphism differs from those of Hobert et al. (2004) for Desert Massasaugas in Colorado (entire range) and in Arizona (Goldberg and Holycross, 1999), as well as reports for Eastern (Seigel, 1986) and Western Massasaugas (Patten, 2006), where no differences were found between adult male and female SVL. This difference in SVL between adult male and female Desert Massasaugas may result from the fact that average daily growth rates for juvenile and adult females is considerably lower than for males of the same size classes, coupled with low survivorship past four years. In *C. atrox*, males and females are equal in size as neonates and grow at similar rates until reproduction; significant sexual size dimorphism does not arise until reproductive maturity (Beaupre et al., 1998; Taylor and DeNardo, 2005). Beyond this point, male *C. atrox* grow more than twice as fast and become appreciably larger than females (Taylor and DeNardo, 2008). Postpartum female Desert Massasaugas collected in the field in fall typically had poor body muscle tone (easily discernable upon palpation of postparturient versus nonreproductive females of equivalent length). A comparison of fall-captured postparturient females with nonreproductive adult females of equivalent length indicated that, for smaller females in particular, reproduction is at a cost to growth and body mass assimilation. Males, contributing significantly less energy directly to reproduction and benefiting from a sex ratio within the population which is close to 1 : 1 (less time spent mate searching), can allocate a greater proportion of resources to growth (Olsson et al., 1997; Taylor et al., 2004; Lind et al., 2010; Smith et al., 2015). The largest Desert Massasauga found in Colorado (SVL = 490 mm, mass = 125 g) was a male from our study site population (Mackessy, 1998); we doubt this is coincidental.

Average clutch sizes for Desert Massasaugas within the study area tend to be lower than previous reports on litter sizes for the species in Arizona and Colorado (range 5 to 7, Lowe et al., 1986; range 4 to 8, Goldberg and Holycross, 1999). At our Colorado field site, litters reached a maximum size comparable to other populations (7 offspring), but the average litter size was quite low (3.3). However, all accounts of clutch size for Desert Massasaugas are considerably lower than reports for Eastern Massasaugas (Goldberg and Holycross, 1999). For example, Keenlyne (1978) reported 11.1 young per female in Wisconsin, and Schuett et al. (1984) reported two litters of Eastern Massasaugas in Michigan with 15 young each. Clutch size differences are likely attributable to the much smaller adult size attained by Desert Massasaugas.

Based on reproductive data for six radioed snakes in southeastern Colorado, and a reproduction study by Goldberg and Holycross (1999), Desert Massasaugas appear to reproduce biennially. Size/age class distributions coupled with biennial reproduction suggest that, on average, an adult female Desert Massasauga in Colorado can be expected to reproduce only once. This indicates that, on average, the total maximum reproductive output of a female over her entire lifetime would be seven offspring (maximum litter size observed for Desert Massasaugas from Colorado), although the actual reproductive output is likely lower.

Desert Massasaugas at this site were observed mating in both the spring and the fall, consistent with reports on Western Massasaugas (Patten, 2006) and also with reports on several other species of North American pit vipers (Aldridge and Duvall, 2002; Rosen and Goldberg, 2002). Observations of six radioed gravid females remaining at the birth site for five to seven days postparturition confirmed that Desert Massasaugas show maternal attendance behavior. Previously, this behavior has not been documented for the species, but it is consistent with increasingly common observations of parental behaviors in viperids (Reinert and Zappalorti, 1988; Butler, 1995; Greene et al., 2002). A female Western Massasauga was found with 11 neonates in pre-shed condition, and several occurrences of females attending neonates have been recorded for Eastern Massasaugas (Swanson, 1930, Reinert and Kodrich, 1982; Johnson, 2000); several postparturient females were observed basking with neonates for several days. At our study site, dispersal of radioed gravid females from birth sites appeared to correspond with neonatal ecdysis and dispersal from the birth site, occurring on the same day as neonate dispersal, which suggests that neonatal ecdysis may be an important cue to mothers (Hoss et al., 2014), suggesting that neonates may follow conspecific scent trails of adults (cf. Reinert and Zappalorti, 1988; Reinert and Rupert, 1999).

The male-male combat we observed in Desert Massasaugas on 27 April 2006 is the first record of male–male combat in this species. Male combat is known to occur among several of the larger rattlesnake species, such as *C. atrox*, *C. horridus*, and *C. viridis* (Klauber, 1956; Gillingham et al., 1983), and this observation in Desert Massasaugas suggests that, like maternal attendance, this behavior is likely a synapomorphy among rattlesnakes. A report by Shepard et al. (2003) described male–male aggression in Eastern Massasaugas in which a male was observed laterally undulating with an elevated body posture, stretching out on top of another male in an effort to gain a superior position. When male snakes must compete directly for females, males tend to be larger, and larger males would predictably have higher reproductive success (Shine, 1994; Smith et al., 2015).

We documented several accounts of predation on Desert Massasaugas in 2005–2006, including two taken by Long-Tailed Weasels, two by Swainson's Hawks, and one by a Northern Harrier. Actual and potential predators of Desert Massasaugas include a wide array of raptorial birds, carnivorous mammals, and several species of snakes. Most hawks, eagles, and owls, both diurnal and nocturnal, are probable predators of Desert Massasaugas, and shrikes may also prey upon them. Badgers (*Taxidea taxus*), Coyotes (*Canis latrans*), and Swift Foxes (*Vulpes velox*) are common mesopredators of snakes in the area, and skunks (*Mephitis* spp.) and Raccoons (*Procyon lotor*) may also feed upon snakes, including massasaugas (Mackessy, 2005). Potential predatory snakes at the Lincoln County site include Racers, Coachwhips, and Milksnakes. Road mortality and direct persecution by humans are also important factors affecting longevity in this population (Hobert et al., 2004, Mackessy, 2005). Because the study site is bisected by a dirt road (oriented north–south), most snakes must cross this road two times per season as they move from and to the hibernaculum area. Although traffic is light on this dirt road, it could represent a significant source of mortality for this population through direct exposure to predators as well as through vehicle-based mortality, and there is a growing recognition of roads as a serious threat to animal conservation generally (e.g., Baxter-Gilbert et al., 2015).

Desert Massasaugas at our study site make long-distance movements (up to 3 km) in the spring from the hibernaculum to summer foraging grounds and then return in the fall. Similar movement patterns have been observed for various other snake species in the study area. This bimodal movement pattern represents migration between hibernation area and summer habitat and is similar in some respects with reports on movement patterns in other populations of massasaugas (Eastern Massasauga: Reinert and Kodrich, 1982; Johnson, 2000; Western Massasauga: Patten, 2006). The dominant habitat type used by Desert Massasaugas for hibernation is a shortgrass prairie association (adjacent to an intermittent stream), with a dense clay soil type; this area also contains the drainage of the site, within 20–30 m of hibernacula. Habitat used by Desert Massasaugas for summer foraging is dominated by an upland mixed-grass/sand sagebrush association and sandy soils. Similar seasonal habitat shifts have been reported in the Eastern Massasauga, and a population in western Pennsylvania hibernated in low-lying wet areas, preferring high-dry areas throughout the summer and fall (Reinert and Kodrich, 1982). Seigel (1986) reported a population of Eastern Massasaugas in northwestern Missouri that used low-lying wet areas (crayfish burrows) for hibernation, moved to dry upland areas in the summer and fall, and then returned to low-lying wet areas before hibernating.

Desert Massasaugas commonly used rodent burrows as hibernacula and showed a high degree of fidelity toward these hibernation sites, returning to nearly the same location from emergence to ingress. Unlike the (often) massive aggregations of snakes at den sites seen among Prairie Rattlesnakes in Colorado (Klauber, 1956; pers. obs., SPM), Desert Massasaugas appear to hibernate individually. Numerous "sinkhole" openings and an intermittent stream occur in the general vicinity of individual Desert Massasauga hibernacula. We observed multiple snake and amphibian species entering these sites in the fall, exiting in the spring and basking in the immediate vicinity shortly before ingress and following egress. Average low temperatures at the study site are well below freezing from December through March and, therefore, snakes must hibernate below frost lines. Stable winter hibernacula are essential for the immediate and long-term survivorship of many ectothermic animals as a way to avoid freezing and to escape predation. For many species of snakes, appropriate hibernacula may be uncommon or nonrandomly distributed, and reports of mixed snake species assemblages at these hibernacula (Gibbons and Semlitsch, 1987; Keller and Heske, 2000) suggest that they may be a limiting component of these populations (Burbrink et al., 1998). We observed a diverse assemblage of amphibians and reptiles at this site, including at least 8 snake species, 5 anuran species, and two species of turtles, suggesting that stable hibernacula are also a limiting resource for these populations.

In studies where there appeared to be extensive habitat overlap among species, resource partitioning has frequently been attributed to alternative niche axes such as time of activity, temperature, or most commonly, food (Seigel and Collins, 1993). Of particular note at our site is the very low prey density at the hibernaculum area relative to the summer foraging grounds (Wastell and Mackessy, 2011), which suggests that food is not the attractive factor. Additionally, the availability of suitable cover/shade in short grass habitat of the hibernaculum is much less than in the sand sagebrush habitat of summer foraging grounds. Stable hibernation conditions, consisting of extensive underground refugia, stable clay-type soils and (relatively) high soil moisture levels, appear to be the primary resource attracting a diverse assemblage of species to this area. Because the winter hibernaculum habitat comprises a small and concentrated resource area, relative to the large and more diffuse area of the summer foraging grounds, it is of particular conservation value and concern.

Based on size/age distribution, low recapture rate ($\sim$6.5% over three years), and short maximum recapture interval (two years or less), overall survivorship of Desert Massasaugas in this population appears to be low, rarely exceeding five years total age. The low number of recaptures of PIT-tagged neonates suggests juveniles may have lower survivorship than do adults, but coupled with apparent low adult maximum age, this could lead to unstable population dynamics and perhaps local extinction. Therefore, it is likely that juvenile survival rates may be considerably higher than expected. Possible factors contributing to lower rates of capture for juveniles include lower detectability attributable to small size and cryptic patterns, high dispersal rates, different behavior patterns, or use of microhabitats where they are relatively protected from predation (Pike et al., 2008). As noted above, the lifetime reproductive output of an average female likely is also quite low. In spite of these limitations, the population studied is robust and may be the largest population of Desert Massasaugas in the entire range of the species. Recruitment to the population via reproduction is likely significant, regardless of low female fecundity, because the population is large, the sex ratio approximates 1 : 1, and total annual reproductive output is 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 (*Cenchris longissimus*), various grasses, and other species (pers. comm., landowners; pers. obs., SPM). Further, we have preliminary data suggesting that shifts in prey abundance are occurring, particularly on the summer foraging sand hills habitat (SPM, unpubl. data). Because Desert Massasauga populations elsewhere are either poorly known (Texas, New Mexico, and Mexico) or in decline (Arizona; see Mackessy, 2005), the Colorado populations are particularly important to the continued persistence of this diminutive species. With increasing pressures such as habitat loss and conversion, human encroachment and global climate change leading to further xerification, these diminutive rattlesnakes may become increasingly threatened in the near future.

Acknowledgments.—We thank the landowners for allowing us access to their property, for countless kindnesses over the years, and for their continuing efforts to conserve this "non-charismatic" species. We thank the many assistants who helped with fieldwork, lab manipulations, and data analysis, including A. Ah-Young, M. Browning, T. Childers, N. Hughes, A. Johnson, J. Leroy, J. Manzer, T. McCabe, and J. Seifert. We thank the Colorado Parks and Wildlife and the US Fish and Wildlife Service for financial support of this project (grant M35455 to SPM). We appreciate the efforts of Jon Runge, biometrician with CPW, for his assistance with program MARK, and Justin Reale, for his assistance with recapture statistics.

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Accepted: 23 February 2016.