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Research Article

Manipulation of Basking Sites for Endangered Eastern Massasauga Rattlesnakes

BRENT D. JOHNSON,[1] *Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA*

JAMES P. GIBBS, *Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA*

THOMAS A. BELL JR., *New York State Department of Environmental Conservation, 1285 Fisher Avenue, Cortland, NY 13045, USA*

KEVIN T. SHOEMAKER, *Department of Natural Resources and Environmental Science, University of Nevada, Reno, 1664 N Virginia Street, Reno, NV 89557, USA*

ABSTRACT Generating open-canopy basking sites via manipulation of vegetative cover has been proposed as a conservation strategy for snakes and other reptiles. We assessed how endangered eastern massasauga rattlesnakes (*Sistrurus catenatus*) responded to 2 types of manipulations at a wetland site in New York, USA: 1) cutting shrubs to create $\leq$100-m^2 plots within known gestation areas in 2008, 2011, and 2012, and 2) cutting tree and shrub cover in the adjacent forest to create a 4-ha forest clearing in 2011. Based on systematic visual surveys from June to August in 2011 and 2012, we estimated snake presence among manipulated and unmanipulated plots in response to plot treatment date. We observed massasaugas selecting newly manipulated plots more often than unmanipulated plots within known gestation areas in both 2011 and 2012, but we detected no increase in massasauga activity within the adjacent forest clearing in either year. The effectiveness of vegetation cutting appeared to decline after 3 years because of vegetation re-growth. We suggest that cutting shrubs to $\leq$0.25 m in height can benefit this population of rare snakes, which faces limited availability of basking sites because of vegetative succession. © 2016 The Wildlife Society.

KEY WORDS crypsis, gestation, *Sistrurus catenatus*, thermal ecology, thermoregulation, vegetation management, wetland succession.

Reduced availability of early successional vegetation types throughout the northeastern United States during the 20th century (Drummond and Loveland 2010) has been implicated in the decline or extirpation of many species (Litvaitis 1993, Brawn et al. 2001, Fuller and DeStefano 2003), including populations of snakes and other reptiles (Johnson and Leopold 1998, Jäggi and Baur 1999, Kingsbury 2002, Smith and Stephens 2003, Fitch 2006). Consequently, vegetation management has been suggested as a potential conservation strategy for rare or endangered snakes. Many studies have indicated that snakes respond positively to reduction of canopy cover (Shoemaker et al. 2009), but investigation of snake response to targeted manipulations of basking sites remains limited (Webb et al. 2005, Pike et al. 2011, Bonnet et al. 2016).

Gravid females of high-latitude, viviparous snake species tend to maintain higher body temperatures than their non-gravid counterparts (Graves and Duvall 1993, Tu and Hutchinson 1994, Foster et al. 2009), often selecting sites with less canopy closure (Reinert 1984, Graves and Duvall 1993, Johnson 1995, Harvey and Weatherhead 2006). Adequate thermoregulation can have demographic consequences by ensuring proper development and viability of young (Lourdais et al. 2004, O'Donnell and Arnold 2005) and by shortening the gestation period of females (Graves and Duvall 1993, Lourdais et al. 2004), which allows postpartum females and neonates more time to forage before hibernation (Charland and Gregory 1990, Burger 1991). Gravid females of viviparous species are also particularly reliant on cryptic basking because of their reduced vagility while gestating (Shine 1980, Seigel et al. 1987, Graves 1989, Schwarzkopf and Shine 1992).

The eastern massasauga rattlesnake (*Sistrurus catenatus*, hereafter, massasauga) is a useful focal species for evaluating the efficacy of targeted basking site manipulations because these snakes thermoregulate mostly via selection of open-canopy microhabitats with or near to ample ground cover (Moore and Gillingham 2006, Harvey and Weatherhead 2010, Bailey et al. 2012). Many massasauga populations are closely associated with isolated, non-forested wetlands (Klauber 1972, Reinert and Kodrich 1982, Seigel 1986, Harvey and Weatherhead 2006, Bailey et al. 2012). The species is listed as Endangered in 9 of 10 states in which it occurs and as Threatened in the province of Ontario (Szymanski 1998). It is a candidate for federal listing in the

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[1] *E-mail: brent.d.johns@gmail.com*

United States under the Endangered Species Act (U.S. Fish and Wildlife Service 2011). It is federally listed in Canada; the Carolinian population was designated Endangered and the Great Lakes-St. Lawrence population Threatened in 2012 (Committee on the Status of Endangered Wildlife in Canada 2012).

In New York State, the eastern massasauga rattlesnake is listed as Endangered, and known from only 2 wetland sites (Szymanski 1998), including Cicero Swamp Wildlife Management Area, the easternmost occurrence of the species. Known gestation areas of gravid female massasaugas at this site have undergone succession to tall woody plant communities within the past half-century (LeBlanc and Leopold 1992). Previous research reported that basking site selection by massasaugas within these areas was influenced by only 2 of 19 environmental variables measured: average daytime environmental temperature and crypsis potential (Shoemaker and Gibbs 2010). Thus, vegetation management producing a mosaic of microhabitat sites for active warming (i.e., direct exposure to solar radiation) and cryptic basking (i.e., minimal exposure by remaining hidden beneath dense ground cover) may facilitate a balance between thermoregulation and predator avoidance for gravid females. Following recommendations from Shoemaker and Gibbs (2010), the New York State Department of Environmental Conservation (NYSDEC) cut small ($\leq 100\ \mathrm{m}^2$) experimental plots among tall (>1.5 m) woody shrubs within known gestation areas of massasaugas at Cicero Swamp. Manipulations occurred in early spring, prior to emergence of the snakes, and were intended to improve basking opportunities, particularly for gestating females. Additionally, the NYSDEC cut all trees and shrubs within 4 ha of adjacent forest. To evaluate the efficacy of these vegetation manipulations in generating high-quality basking sites for massasaugas, we 1) determined whether adult massasaugas selected manipulated plots for basking more often than nearby unmanipulated plots, 2) compared the quality of these plots based on the 2 key habitat characteristics influencing basking site selection by massasaugas (daytime environmental temperatures and crypsis potential; Shoemaker and Gibbs 2010), and 3) evaluated the use of manipulated plots by adult massasaugas as active warming or cryptic basking sites.

STUDY AREA

Cicero Swamp Wildlife Management Area is a 2,003-ha wetland complex in Onondaga County, New York, USA owned and managed by the NYSDEC. The site lies at 122 m elevation and has a continental and humid climate. It is composed of red maple (*Acer rubrum*) swamp, swamp forest (mostly black spruce, tamarack, and red maple), upland mixed hardwood forest, and upland field. Overwintering and gestation of massasaugas at the site occurred primarily within a 37-ha shrub-dominated peatland (Johnson 2000) that underwent succession to dense, tall woody shrubs and forest after a 6-month fire in 1892 burned off 1 m of its peat layer in some areas (LeBlanc and Leopold 1992). This so-called burn area was previously dominated by herbaceous and low shrub vegetation but experienced substantial recolonization by black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in the past half-century (Johnson 2013). Gestation areas of gravid female massasaugas occurred at the northern and southern edges of the burn area, which generally contained tall (>1.5 m) shrubs (mostly highbush blueberry [*Vaccinium corymbosum*], mountain holly [*Ilex mucronata*], and black chokeberry [*Aronia melanocarpa*]), and more potential underground retreat sites than surrounding areas (Johnson 1995, Shoemaker 2007). These retreat sites included cavities within elevated root systems (i.e., hummocks), which likely also served as overwintering sites for the entire population. Ground cover within the gestation areas was primarily bryophytes (*Sphagnum* spp. and *Polytrichum* spp.; Johnson 2000). Although non-gravid adult massasaugas typically spent the active season in the surrounding swamp and upland forests, gravid females remained in the gestation areas and moved an average of only 7.1 m/day (Johnson 2000).

METHODS

Plot Use Surveys

In late summer 2008, managers reduced canopy cover in 6 28.3-m^2 experimental plots in 1 gestation area by cutting shrubs with hand tools to <0.25 m in height. All fallen vegetation was then removed from the plots to maximize sunlight exposure at ground level and ease survey efforts. In early spring 2011 (prior to the emergence of massasaugas), managers used mechanical tools to create 16 100-m^2 plots in each of the 2 known gestation areas, and to cut all trees and shrubs within 4 ha of adjacent mature forest. All fallen vegetation was left in place within forest clearings. In early spring 2012, managers cleared shrub vegetation to create 6 new 28.3-m^2 plots among existing plots in each of the 2 gestation areas.

For comparisons with manipulated plots, we established 28 28.3-m^2 uncut survey plots among the gestation-area plots by selecting previously recorded massasauga basking sites (Shoemaker 2007) or sites with relatively low shrubs (Fig. 1). Additionally, we designated 16 36-m^2 survey plots within the forest clearing and 16 similarly sized plots in the nearby forest periphery. We searched for surface-active, adult massasaugas within all survey plots from 22 June to 24 August 2011 and 21 May to 23 August 2012. Two experienced observers systemically searched the entirety of each survey plot, circling the perimeter before moving into the center, once per week in 2011. Three observers performed identical searches in 2012. Surveys started at approximately 0830 hours and typically ended before 1300 hours, with all surveys in each gestation or forest clearing area occurring on the same day. To account for a potential effect of time of day on our ability to detect aboveground snakes, we varied the order in which we surveyed plots in each area from week to week.

We detected snakes within plots by sight or hearing their rattle and captured them using snake tongs. We placed each captured snake in a large bucket and allowed it to enter into a clear plastic tube (~2.5–5 cm diameter). While holding the

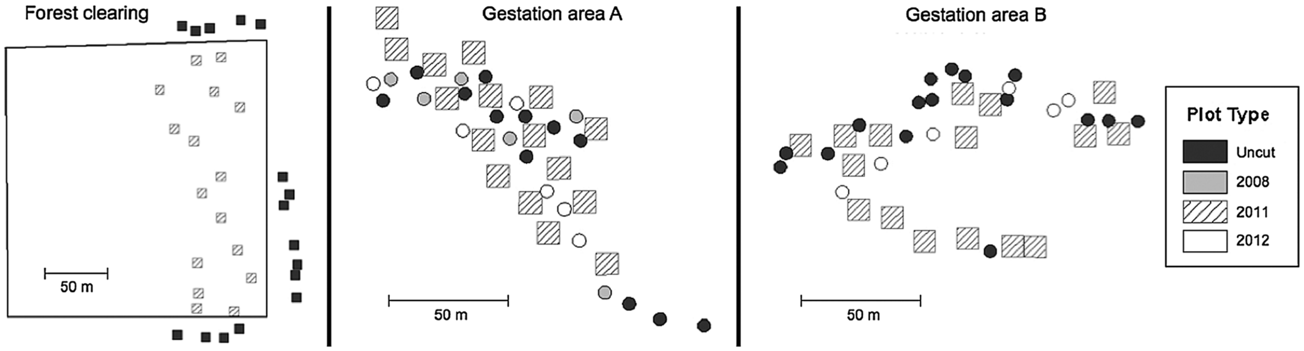

Figure 1. Spatial arrangement of survey plots within the 2 gestation areas and forest clearing at Cicero Swamp Wildlife Management Area, New York, USA. Survey areas were separated by <500 m. Plots are categorized by the years in which they were cut.

snake approximately halfway within the tube, we verified its sex using a sexing probe and, if female, determined its reproductive condition by palpating for multiple lumps in the lower abdomen as evidence of the presence of oviductal eggs (Johnson 1995). We measured snout-vent length (SVL) of each individual using a flexible measuring tape and determined its mass by placing it in a cloth bag and using a spring scale (Pesola® Medio-Line 41000; Pesola AG, Baar, Switzerland). Because we found no gravid females <40 cm SVL, we assumed individuals shorter than this length to be juveniles and excluded them from analyses. To ensure that we did not detect the same individual within multiple plots in the same day, we marked each adult massasauga through injection of a Passive Integrated Transponder tag (AVID Identification Systems, Inc., Norco, CA, USA) for permanent identification (Jemison et al. 1995). All work was conducted under the State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee Protocol (120303).

We used generalized linear mixed models (glmmADMB package; Fournier et al. 2012) with a negative binomial error distribution (to accommodate zero-inflated data; Bolker 2008) in R (Version 3.1.1, www.r-project.org, accessed 10 Aug 2014) to model the density of adult massasaugas above ground within survey plots (snakes/100 m^2) each survey day as a function of plot type, which corresponded to the year in which a plot was treated: 2008, 2011, 2012, or if it remained uncut. Because of re-growth of vegetation in cut plots during our first (2011) field season, we analyzed survey data from 2011 and 2012 separately to simplify comparison of snake density among plots in relation to plot age as opposed to actual year of plot treatment. Because we surveyed in various weather conditions (excluding heavy rain) to maximize the number of survey days each season, we included a set of daily weather variables readily obtained from data reported by a nearby weather station ($\sim$7 km away at Hancock International Airport, Syracuse, NY, USA) within our models to account for their possible effects on observed massasauga densities. Daily weather variables included maximum ambient temperature, precipitation, and presence of adverse weather conditions (e.g., fog, haze, or thunderstorm, the 3 prevailing conditions in the area). Incorporating average daily weather conditions for each survey day, as opposed to conditions strictly during survey hours, accounted for variation in weather across each survey season, but did not allow for precise interpretation of the influence of these variables on observed massasauga densities. Including plot number as a random effect in each model simulated repeated measures analysis and accounted for the potential influence of plot location on snake densities (Crawley 2007). We selected the best model for each field season based on the smallest Akaike's Information Criterion scores (AIC; Burnham and Anderson 1998) and interpreted the influence of individual parameters within each model based on the significance of corresponding coefficient estimates ($\alpha = 0.05$). We used predicted density values from the best model for each season to compare average densities of massasaugas among plot types (2008, 2011, 2012, and uncut). A tendency for snakes to flee as we approached precluded use of methods for estimating detection rates (e.g., a double-observer approach) among plot types. Therefore, our models assumed 100% detection of surface-active snakes within all survey plots. Assuming high detection rates for all plot types was likely reasonable because all plots were small in size (28–100 m^2), with little to no leaf litter and shrub cover averaging <0.5 m in height. Additionally, each survey was conducted by 2 to 3 observers who could detect snakes by either sight or sound, and typically did so within 2 m of a snake regardless of plot type.

Comparing Quality of Plots as Basking Sites

We measured environmental temperatures and crypsis potential in 2012 to estimate basking site quality in relation to plot type. To do so, we recorded hourly environmental temperatures (T_e) with 30.5-cm painted copper pipe models containing dataloggers (iButton®; Maxim Integrated Products, Sunnyvale, CA, USA) following Shoemaker and Gibbs (2010). Temperatures recorded by such models are positively correlated with actual body temperatures of co-occurring basking snakes (Shoemaker and Gibbs 2010). Models were left in the centers of plots, which we assumed to have maximal daily exposure to sunlight, in 1 of the 2 gestation areas (4 plot types × 5 plots = 20 models) and the forest clearing and peripheral forest areas (2 plot types × 5 plots = 10 models) from 30 May to 13 August 2012. We used the recorded temperature data to calculate a variable highly relevant to basking site selection of massasaugas: average daytime T_e (0700–1900 hours; Shoemaker and Gibbs 2010). We also determined average number of hours per day above the lower bound of the daytime thermal set-point range (T_{set}) for massasaugas (28.4° C, representing the 25% quartile of daytime temperatures selected by massasaugas in a laboratory thermal gradient; Harvey and Weatherhead 2011) but used average daytime T_e as a primary indicator of basking site quality because the 2 temperature variables were highly correlated ($R^2 = 0.92$). We compared average daytime T_e among plot types using an analysis of variance (ANOVA).

To measure the crypsis potential provided by the various plot types, we used a physical model made from a 0.5-m white polyvinyl chloride pipe approximately 2.5 cm in diameter and striped with black electrical tape. At random locations ($n = 3$) in each plot in mid-summer, we determined average crypsis (lack of visibility) of the model based on 3 visual estimates, made at standing height, ranked on a 0 to 5 scale (crypsis index; Shoemaker and Gibbs 2010). After first estimating the crypsis of actual basking massasaugas and the model subsequently in the same location, we found log-transformed crypsis for the model to be predictive of the crypsis of actual massasaugas ($n = 42$, $R^2 = 0.76$, $P < 0.001$). Therefore, we used the resulting least squares linear equation, explaining the relationship (massasauga crypsis potential $= 0.966 + 5.674 \times \log$ [(crypsis index) + 1]) to convert the average crypsis estimates for plots into massasauga-specific crypsis potential values, which we then contrasted among plot types using an ANOVA.

Evaluating Use of Plots as Active Warming and Cryptic Basking Sites

To further elucidate the importance of active warming and cryptic basking sites for thermoregulation by massasaugas and the ability of vegetation cutting to generate both of these microhabitat characteristics, we first compared the time to maximum T_e and maximum T_e achievable between sun-exposed and shaded sites within manipulated plots. We did so using brown, clay models ($n = 12$), 4 cm in diameter and 10 cm in length, containing iButton® dataloggers and chilled to approximately 2° C. We placed these models in paired sun-exposed and shaded locations (<1 m apart) in 6 different 0-year-old plots (cut in 2012) at 1200 hours on a cloudless day. The models logged temperatures every 1 minute, enabling us to use paired sample *t*-tests to compare warming times and maximum T_e achievable between the sun-exposed and shaded locations. Additionally, for each massasauga found within a survey plot, we visually estimated its percent exposure, from standing height to the nearest 10%, and measured its surface body temperature by averaging 3 dorsal readings of an infrared (IR) thermometer (Extech® IR400; Extech Instruments, Waltham, MA, USA). We then correlated exposure and temperature values for observed snakes to enable comparisons to the temperature performance of sun-exposed and shaded clay models.

RESULTS

Plot Use Surveys

In 2011, we made 155 sightings of adult massasaugas, including 29 marked individuals (25 gravid females) within surveyed plots. In 2012, 73 sightings in the gestation areas included 22 marked individuals (12 gravid females). Gravid females accounted for at least 86% of sightings in 2011 (with 12% of snakes unidentified) and 73% of sightings in 2012 (with 5% unidentified). Individuals were not captured more than once in a single day. In the forest clearing in 2012, we had a single sighting of an adult male in a survey plot and found a gravid female and non-gravid adult female outside of survey plots. The best model for the 2011 season suggested that variance in the density of massasaugas recorded each survey day was explained by plot type and our set of daily weather variables: maximum air temperature, precipitation, and presence of adverse weather conditions (Table 1). However, individual parameter coefficients indicated that massasauga densities were driven by plot type and presence of adverse weather conditions but not by maximum air temperature (range = 20.6–38.3° C) or precipitation within the same day (Table 2). Predicted average density of massasaugas in 2011 did not differ between 0-year-old plots (cut in 2011; $\bar{x} = 0.1413$ snakes/100 m^2, SE = 0.0036, $n = 280$) and 3-year-old plots ($\bar{x} = 0.1325$ snakes/100 m^2, SE = 0.0065, $n = 63$) but was higher in each of these plot types than it was in uncut plots ($\bar{x} = 0.0034$ snakes/100 m^2, SE = 0.0001, $n = 238$), which generated only 1 massasauga sighting. The best model for 2012 also included plot type and daily weather variables (Table 1), although precipitation and adverse weather conditions did not affect massasaugas densities based on parameter coefficient estimates (Table 2). In this season, an interaction between plot type and maximum air temperature (range = 17.2–38.3° C) explained the observed massasauga densities such that, at higher maximum air temperatures, we recorded greater massasauga densities in more recently cut plots. In this second field season, predicted average densities of massasaugas in 0-year-old plots (cut in 2012; $\bar{x} = 0.0720$ snakes/100 m^2, SE = 0.0020, $n = 168$) and 1-year-old plots ($\bar{x} = 0.0450$ snakes/100 m^2, SE = 0.0006, $n = 448$) were higher than in uncut plots ($\bar{x} = 0.0085$ snakes/100 m^2, SE = 0.0009, $n = 392$). Density of massasaugas in 4-year-old plots ($\bar{x} = 0.0130$ snakes/100 m^2, SE = 0.0028, $n = 84$) did not differ from that of uncut plots.

Comparing Quality of Plots as Basking Sites

In mid-season 2012, average shrub height varied among gestation-area plot types (ANOVA; $F_3 = 21.4$, $P \leq 0.001$). Compared to vegetation measured in uncut plots (48.3 ± 10.3 cm SD, $n = 28$), shrub height averaged 23.5 cm lower in 0-year-old plots (24.8 ± 4.5 cm SD, $n = 12$, $t = -7.7$, $P \leq 0.001$). Shrubs were also lower in 1-year-old plots (38.1 ± 9.1 cm, $n = 32$, $t = -4.4$, $P \leq 0.001$) and 4-year-old plots (33.0 ± 5.6 cm, $n = 6$, $t = -3.9$, $P \leq 0.001$) relative to uncut plots. Vegetation measured within plots in the 1-year-old forest clearing (29.1 ± 9.1 cm, $n = 32$) was slightly lower, on average, than that of similarly aged plots in the gestation

Table 1. Best candidate generalized linear mixed models describing massasauga densities among plot types at Cicero Swamp Wildlife Management Area, New York, USA in 2011 ($n = 1092$) and 2012 ($n = 581$). Plot type refers to survey plots created in the following years: 2008, 2011, 2012, and uncut. Max temp refers to maximum daily temperatures. Precipitation refers to daily rainfall (cm). Weather indicates the presence of ≥ 1 of 3 prevailing weather conditions: fog, haze, and thunderstorm.

Variables included	Log likelihood	K[a]	ΔAIC[b]	Akaike weight[c]
2011				
Plot type, max temp, precipitation, weather	−254.79	8	0.0	0.890
Plot type	−259.86	5	4.1	0.110
Max temp, precipitation, weather	−266.97	6	20.4	≤0.001
Null	−271.79	3	24.0	≤0.001
2012				
Plot type × max temp, precipitation, weather	−298.10	12	0.0	0.755
Plot type	−305.45	6	2.7	0.195
Null	−310.49	3	6.8	0.025
Max temp, precipitation, weather	−307.51	6	6.8	0.025

[a] K = number of estimable parameters in the model.

[b] ΔAIC = difference between Akaike's Information Criterion (AIC) of each model and AIC of the best model in the set.

[c] Akaike weight = estimate of relative model strength.

areas. Daytime T_e (averaged over days recorded) in 2012 also varied among most plot types (ANOVA; $F_3 = 9.9, P \leq 0.001$), with 0-year-old plots ($30.9 \pm 1.7°$ C SD) averaging 5.3° C warmer than uncut plots ($25.6 \pm 2.1°$ C, $t = 5.4$, $P \leq 0.001$; Fig. 2). Compared to the average daytime T_e of uncut plots, temperatures were also higher in 1-year-old plots ($28.1 \pm 1.1°$ C SD, $t = 2.6$, $P = 0.02$) and 4-year-old plots ($27.9 \pm 1.1°$ C, $t = 2.3$, $P = 0.03$) but were similar between these 2 plot types. Only 0-year-old plots provided temperatures well above the lower T_{set} range for massasaugas (28.4° C; Fig. 2). Additionally, average daytime T_e recorded in the forest clearing ($31.1 \pm 2.0°$ C) was similar to that of the 0-year-old plots in the gestation area. Compared to those of uncut plots, daytime temperatures were above 28.4° C an average of 2.0 hours longer each day in 1- and 4-year-old plots and 2.9 hours longer each day in 0-year-old plots.

Table 2. Coefficients estimated for the highest-ranked candidate generalized linear mixed models describing massasauga densities among plot types at Cicero Swamp Wildlife Management Area, New York, USA in 2011 ($n = 1092$) and 2012 ($n = 581$). Plot type refers to survey plots created in the following years: 2008, 2011, 2012, and uncut (shown as the intercept). Max temp refers to maximum daily temperatures. Precipitation refers to daily rainfall (cm). Weather indicates the presence of at least 1 of 3 prevailing weather conditions: fog, haze, and thunderstorm. Plot number, the identity of individual plots, was included as a random effect and had a variance of 2.600 ± 1.612 SD in 2011 and a variance of 3.385 ± 1.840 SD in 2012.

Coefficients	Estimate	SE	Z	P
2011				
Intercept	−6.661	1.912	−3.48	≤0.001
Plot type 2008	3.541	1.161	3.05	0.002
Plot type 2011	3.710	0.921	4.03	≤0.001
Max temp	0.006	0.020	0.31	0.753
Precipitation	0.075	0.152	0.49	0.623
Weather	0.800	0.303	2.64	0.008
2012				
Intercept	7.738	5.237	1.48	0.140
Plot type 2008	−1.332	10.334	−0.13	0.897
Plot type 2011	−10.165	5.691	−1.79	0.074
Plot type 2012	−12.778	6.470	−1.98	0.048
Max temp	−0.162	0.067	−2.44	0.015
Precipitation	−0.141	0.648	−0.22	0.828
Weather	0.580	0.373	1.56	0.120
Plot type 2008 × max temp	0.020	0.132	0.15	0.878
Plot type 2011 × max temp	0.151	0.072	2.11	0.035
Plot type 2012 × max temp	0.188	0.080	2.34	0.019

Predicted massasauga crypsis potential varied among some gestation-area plot types (ANOVA, $F_3 = 14.9, P \leq 0.001$) such that uncut plots provided higher crypsis potential (crypsis = 3.5 ± 0.8 SD) than 0-year-old plots (crypsis = 2.0 ± 0.5, $t = -6.3$, $P \leq 0.001$) and 1-year-old plots (crypsis = 2.7 ± 0.6, $t = -4.4, P \leq 0.001$; Fig. 2). However, crypsis potential did not differ between uncut plots and 4-year-old plots (crypsis = 3.1 ± 0.9 SD, $t = -1.3$, $P = 0.21$). All plot types provided some amount of crypsis potential close to that selected by massasaugas, on average, in 2012 (crypsis = 2.3 ± 1.7, $n = 42$).

Evaluating Use of Plots as Active Warming and Cryptic Basking Sites

Average maximum temperature reached by sun-exposed (i.e., actively warming) clay models was 9.9° C higher (±3.5° C SD) than that of shaded (cryptic basking) models (paired sampled t-test, $t_5 = 6.9$, $P = 0.001$), and was 11.6° C above the maximum ambient temperature. Sun-exposed models achieved maximum temperatures about 1 hour faster (±0.8 hr SD, $t_5 = 3.1$, $P = 0.03$) than shaded models. Percent exposure of massasaugas found in plots was negatively correlated with T_{IR} measurements in 2011 (Pearson's correlation coefficient = −0.70, $P \leq 0.001$) and 2012 (Pearson's correlation coefficient = −0.32, $P = 0.007$), indicating that cryptically basking massasaugas had higher body temperatures than actively warming individuals. Average T_{IR} of massasaugas within survey plots at time of capture was 26.0° C (±5.1° C) in 2011 and 26.6° C (±4.3° C) in 2012. Average exposure of these massasaugas was 62.4% in 2011 and 57.8% in 2012, but most sightings in each season were of snakes closer to either 0% or 100% exposure (Fig. 3).

DISCUSSION

Experimental replication and interspersion of plots of varying shrub height at Cicero Swamp provided strong evidence (Smallwood et al. 1999) that massasaugas basked

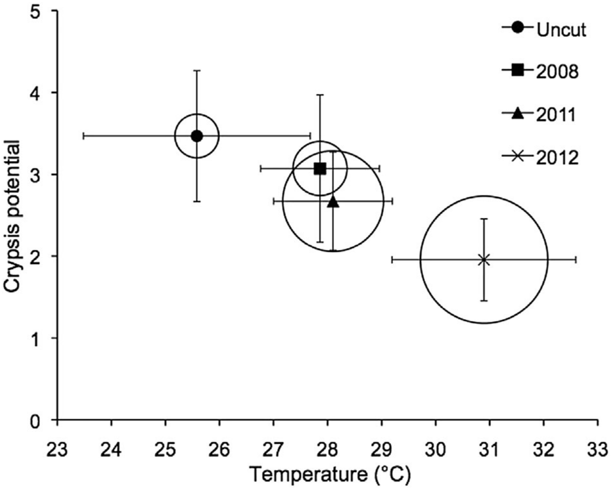

Figure 2. Mean daily environmental temperature (T_e; recorded with physical operative temperature models in 5 plots/plot type) and crypsis potential (i.e, ability to remain hidden from visual predators; based on 3 visual estimates of a model within each plot) of different plot types in the gestation areas of Cicero Swamp Wildlife Management Area, New York, USA in 2012. Bars on points represent standard deviations. The size of circles surrounding points reflect relative densities of massasaugas observed for each plot type in the same season (0.0085–0.0720 snakes/100 m^2).

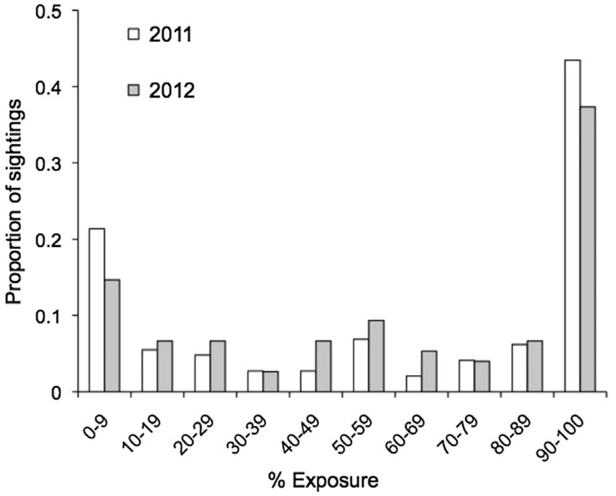

Figure 3. Percent exposure of massasaugas within survey plots in 2011 ($n = 145$) and 2012 ($n = 75$) at Cicero Swamp Wildlife Management Area, New York, USA.

more often in plots with manipulated shrub cover than in unmanipulated plots. Our results indicate that cutting shrubs to ≤0.25 m in height generated high-quality basking sites, with improved thermal properties and adequate crypsis potential (Shoemaker and Gibbs 2010), within the established wetland gestation areas of this population. We conclude that there is value in canopy cover removal for managing this population of snakes threatened by vegetative succession, and recommend further research, particularly population and habitat viability analyses (Lacy et al. 2014), to determine the extent of vegetation manipulation necessary for supporting a target population size.

Massasaugas at Cicero Swamp likely used manipulated plots mostly to increase their body temperature, rather than to sustain a high body temperature after reaching it, and became more cryptic by entering retreat sites soon after warming to a desired body temperature (Shoemaker and Gibbs 2010). We observed that massasaugas had access to a wide thermal gradient, often preferred by snakes for basking (Spellerberg 1975, 1988), even within newly manipulated plots (sun-exposed models achieved a maximum temperature 9.9° C higher than shaded models within these plots, and did so 1 hr earlier). Moreover, we detected snakes that typically had either a high or low, but not intermediate, degree of exposure while basking. Although Harvey and Weatherhead (2010) observed massasaugas at their northern range limit in Upper Bruce Peninsula, Ontario, Canada spending >70% of their time basking, we suspect that basking site manipulations and warmer ambient temperatures at our more southern location allowed massasaugas to spend more of each day sequestered within retreat sites. Many other temperate-zone reptiles have been observed to spend only limited time above ground (Avery 1976, Huey 1982, Huey et al. 1989) or basking (Blouin-Demers and Weatherhead 2001, Row and Blouin-Demers 2006) each day, presumably to address the tradeoff between thermoregulation and predator avoidance.

We found all manipulated plots within the gestation areas provide adequate crypsis potential for massasaugas; shrubs cut to ground level grew to nearly 0.25 m in height by the middle of the next growing season. Therefore, cutting shrubs is unlikely to result in excessive exposure of snakes to visual predators. Furthermore, natural underground retreat sites were plentiful across the study site and unaffected by shrub cutting. Underground retreat sites can provide refuge from predators (Webb and Whiting 2005) and extreme temperatures (Huey et al. 1989) and are typically found near basking sites of massasaugas (Harvey and Weatherhead 2006, Marshall et al. 2006, DeGregorio 2008) and other snake species (Burger and Zappalorti 1988, Nilson et al. 1999). Although we likely failed to detect snakes that were below ground within our survey plots at Cicero Swamp, we varied the order of plot surveys to avoid biasing our ability to detect aboveground snakes among plot types. Additionally, we suspect that any snakes underground had already warmed to desired temperatures; these snakes most likely occupied newer, warmer, and more exposed plots prior to retreating, potentially causing us to underestimate the true effects of basking site treatments on snake densities among plot types. Similarly, handling of snakes may have reduced our ability to recapture individuals across each survey season (Parent and Weatherhead 2000, Brown 2008) but would have most notably affected detection within newer plots, where we captured snakes most often. Further study could be useful for evaluating potential effects of vegetation manipulations on subsurface temperatures and the daily thermoregulatory behavior of snakes.

We observed no regular use of a forest clearing outside of (but adjacent to) known massasauga gestation areas, similar to a study of massasaugas in northern Michigan (DeGregorio 2008). Other studies have detected higher numbers of at least some snake species in response to logging activities without specifying any changes in basking behavior (Ross et al. 2000, Crosswhite et al. 2004, Shipman et al. 2004). It is unclear if clearing trees and shrubs in the swamp forest adjacent to established gestation areas at Cicero Swamp failed to generate high-quality basking sites or if gravid female massasaugas, which represented most of our sightings within the gestation areas, simply will not extend their active-season range within 2 years because of their reduced vagility while gestating (Shine 1980, Seigel et al. 1987) and, possibly, fidelity to gestation sites or natal homing. We suspect the latter because environmental temperatures recorded within the clearing were similar to those in the most regularly used gestation-area basking sites. We also suspect that similar surveys conducted years or decades in the future could document higher use of the forest clearing by adult massasaugas because individuals may gradually shift their home ranges among active seasons.

Because vegetation cutting in established basking areas can increase the speed at which snakes achieve desired body temperatures, thereby enabling snakes to devote more time to predator avoidance (e.g., in retreat) or foraging, basking site enhancement activities may serve to improve the lifetime fitness of females. Also, adequate thermoregulatory opportunities can improve fitness of young (Lourdais et al. 2004, O'Donnell and Arnold 2005), with positive consequences for population recruitment rates. Long-term monitoring is necessary to elucidate such outcomes, however, and improvements to population viability should ultimately be the documented outcome of vegetation management efforts if their value as a long-term conservation strategy is to be realized (Shoemaker et al. 2009).

MANAGEMENT IMPLICATIONS

We conclude that clearing shrub vegetation within established gestation areas can generate high-quality basking sites for massasaugas at Cicero Swamp. We propose mechanical cutting of all shrubs to ≤ 0.25 m above ground level within delimited areas, but recommend further research (e.g., a population and habitat viability analysis) to determine the amount of cutting needed to support a target population size. All cutting should occur in late winter or early spring, prior to the spring emergence of massasaugas, to reduce risk of inadvertent harm to snakes, and should be undertaken routinely (or at least every 3 years at Cicero Swamp, based on differing use of 2008-cut plots between 2011 and 2012) to compensate for re-growth of vegetation among seasons. Although basking sites appear to be used less as shrubs grow toward 0.5 m in height, shrub cover remains lower in cut plots than in surrounding areas at our study site for up to 10 years (Johnson and Breisch 1999). Therefore, extended intervals between manipulation events could still potentially prove beneficial to massasaugas as long as manipulated sites provide some thermal advantage relative to uncut sites. Burning of fallen vegetation and application of herbicides at the time of cutting have been shown to slow vegetation re-growth at Cicero Swamp for several subsequent seasons, but neither additional strategy has resulted in more lasting effects on vegetative growth and succession than simple cutting (Johnson and Leopold 1998). Lastly, manipulation of forest cover in adjacent areas does not appear to generate as much snake response within 2 subsequent active seasons as does manipulation of shrub cover within known gestation areas.

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