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Management and Conservation Article

Evaluating Basking-Habitat Deficiency in the Threatened Eastern Massasauga Rattlesnake

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ABSTRACT Woody plant succession is hypothesized to threaten many reptile populations by reducing the amount of solar energy available for thermoregulation. Mitigation via vegetation management is often recommended; however, the need for such management practices rarely has been evaluated. We examined the need for basking-site enhancement for the eastern massasauga rattlesnake (*Sistrurus c. catenatus*; hereafter EMR) in New York, USA, where only 2 populations remain: one at an open-canopy site and another at a closed-canopy site. Microhabitat temperatures were substantially lower at the closed-canopy site, where EMRs selected the warmest available basking sites. Eastern massasauga rattlesnakes in the open-canopy population selected basking sites that afforded greater cryptic cover. We recommend experimental reduction of shrub cover to improve EMR basking habitat at the closed-canopy site. More generally, we caution that management efforts to reduce shrub cover for basking EMRs should maintain adequate cryptic cover.

KEY WORDS basking-site restoration, crypsis, eastern massasauga rattlesnake, habitat management, New York, operative temperature, *Sistrurus catenatus*, thermoregulation.

Thermoregulation is a key factor influencing habitat selection in reptiles (Stevenson 1985, Reinert 1993). Reforestation can pose a threat to reptile populations in forest-dominated landscapes, because many reptiles are dependent on patches of open-canopy habitat for thermoregulation (e.g., Trani 2002). Examples include the disappearance of several asp viper (*Vipera aspis*) populations in the Jura Mountains of Switzerland (Jäggi and Baur 1999), the apparent extirpation of 4 native snake species and the decline of 8 others from the Fitch Natural History Reservation in Kansas, USA (Hall 1994, Fitch 2006), the extirpation of 2 lizard populations in the prairie sandhills of Nebraska, USA (Ballinger and Watts 1995), and terrestrial reptile declines in the northeastern United States (Litvaitis 1993, Brawn et al. 2001).

Woody-plant succession can be managed with techniques such as prescribed fire (Wright and Bailey 1982), flooding (Michener and Haeuber 1998), herbicide application (Wigley et al. 2000), mowing (Parr and Way 1988), brush-clearing (Johnson and Leopold 1998), and timber harvesting (Annand and Thompson 1997). Such practices can unintentionally threaten snake species, however, by degrading habitat quality or by reducing protective cover and thereby increasing predation rates (e.g., Setser and Cavitt 2003, Pearson et al. 2005). Many snake and lizard species rely on crypsis to avoid predators (Bauwens and Thoen 1981, Schwarzkopf and Shine 1992, Parent and Weatherhead 2000). When basking, these species generally use dense ground cover and cryptic coloration to escape detection (Nilson et al. 1999, Casper et al. 2001, Melville and Swain 2007). Thus, vegetation management can result in demographic benefits (e.g., increased growth rate and improved reproductive success) due to improved thermal environment (Seigel and Ford 1987). However, vegetation management can also result in less apparent, and rarely evaluated, demographic costs associated with loss of cover and subsequent increased mortality.

The eastern massasauga rattlesnake (*Sistrurus c. catenatus*; hereafter EMR) persists as 2 isolated population remnants at the eastern edge of the species' geographic range, and is an apparent case of a reptile species threatened by woody-plant encroachment (Wright and Wright 1957). The EMR is a medium-sized (approx. 47–100-cm-long), ovoviviparous snake favoring open-canopy, early succession habitat (Johnson and Leopold 1998). The association of EMRs with open-canopy habitat likely reflects the thermoregulatory needs of gravid females (Reinert and Kodrich 1982, Johnson 1995). Gravid females of this species, like many other temperate-zone, live-bearing snake species (e.g., Tu and Hutchison 1994), generally maintain greater body temperatures than their nongravid counterparts via extensive above-ground basking behavior (Reinert and Kodrich 1982). When above ground, EMRs employ cryptic coloration and behavior to avoid detection by predators (Parent and Weatherhead 2000). The EMR is listed as threatened or endangered throughout its range, where it is generally relegated to isolated habitat remnants. Forest regeneration following the hypsithermal prairie expansion (approx. 8,000 yr ago, when open-canopy prairie dominated much of the Great Lakes Region of the United States) probably contributed to population isolation (Beltz 1993, Cook 1993). Drainage and development of wetlands has exacerbated the decline of the EMR (Wright 1941).

Woody plants have steadily recolonized the easternmost location, Cicero Swamp, after an 1892 fire, and some experts believe that basking habitat has become a critical

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limiting resource for EMRs at this site (Johnson and Breisch 1999). The hypothesis of basking-site limitation has rarely been tested for any reptile population (but see Webb et al. 2005) and has never been tested for the EMR. With expensive vegetation-management interventions proposed for Cicero Swamp (Johnson and Breisch 1999) and other habitats supporting rare reptiles (e.g., Vollmar Consulting 2005), it is important to critically evaluate the hypothesis of thermal limitation. The risk of artificially increasing detection rates (by humans or other species) through management also must be evaluated, because poaching and predation can threaten populations of EMRs and other rare reptiles (e.g., Brown 1993, King et al. 2004).

To test whether warm basking sites represent a limiting resource for EMRs at Cicero Swamp, we 1) evaluated whether relative warmth was a key factor influencing basking-site selection by EMRs at Cicero Swamp, 2) evaluated the degree to which microhabitat characteristics other than warmth (e.g., canopy closure, shrub ht, woody-stem density) explained basking-site selection at Cicero Swamp, and 3) contrasted average basking-site conditions at Cicero Swamp with a nearby population (Bergen Swamp) that occupies open-canopy habitat. We also evaluated the likely positive and negative effects of vegetation management by assessing how manipulation of key habitat characteristics (e.g., canopy openness, canopy ht) was likely to alter environmental temperature and the ability of snakes to remain hidden from visual predators.

STUDY AREA

We surveyed the only 2 extant populations of EMRs remaining in New York: Cicero Swamp and Bergen Swamp. Cicero Swamp was a large (approx. 2,024-ha) wetland complex located 15 km northeast of Syracuse, New York, USA. Primary EMR habitat at Cicero Swamp was a 37-ha shrub-land flanked by red maple swamp, swamp forest (forested peat-land), upland forest, and upland field. The shrub-land habitat (known as the burn area) occurs in the footprint of a fire that consumed nearly a meter of peat in 1892 (LeBlanc and Leopold 1992) and is currently dominated by the tall (>1.5-m) shrubs *Vaccinium corymbosum*, *Nemopanthus mucronata*, and *Aronia melanocarpa* (Johnson 1995). Bergen Swamp was a wetland complex located approximately 150 km due west of Cicero Swamp and contained less than half the total wetland acreage of Cicero Swamp. Eastern massasauga rattlesnake habitat at Bergen Swamp was comprised of 4 distinct habitat types: marl fen (primary habitat), red maple swamp, upland forest, and upland field. Primary EMR habitat at Bergen Swamp was an open-canopy marl fen (approx. 16 ha) dominated by sedges and sparsely distributed with hummocks of short (<0.5-m) shrubs (mostly *Dasiphora floribunda* and *Juniperus* spp.). The open-canopy marl fen at Bergen Swamp contrasted sharply with primary EMR habitat at Cicero Swamp, presenting an opportunity to compare patterns of basking-site selection at 2 sites with substantially different levels of canopy closure.

METHODS

Population Surveys

Because a dense shrub layer severely constrained researcher movement at Cicero Swamp, we cut a permanent survey trail (approx. 1 m wide and 3 km long) manually through core habitat (the burn area at Cicero Swamp and the marl fen at Bergen Swamp) and peripheral habitat. We established a similar trail at Bergen Swamp (approx. 3.5 km long) to replicate the methods used at Cicero Swamp, although no trail-clearing was necessary. We designed survey trails to sample each major habitat type available to snakes, with survey coverage greatest for core habitats.

Eastern massasauga rattlesnake surveys were conducted by ≥ 2 experienced observers at both sites approximately 2 times/week during 15 May to 15 September 2006. We classified snakes initially observed in a coiled resting posture as basking. We defined basking sites as the locations at which basking observations occurred, and we classified aggregations of ≥ 2 EMRs as a single basking site. We determined sex with sexing probes (J. Lázló, San Antonio Zoological Gardens and Aquarium, unpublished report [1973]) and we determined reproductive condition by palpating for oviductal eggs (see Johnson 1995). We measured surface body temperature of all snakes by recording the average of 3 dorsal infrared (IR) thermometer readings (Extech® RH101; Extech Instruments, Waltham, MA). We also measured mass and snout–vent length, and we injected Passive Integrated Transponder tags (AVID Identification Systems, Inc., Norco, CA) to permanently identify individuals (Jemison et al. 1995). Our research protocols were approved by the State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee (protocol no. 2006-03).

Contrasting Environmental Temperature Between Basking Sites and Random Sites

We measured environmental temperature (T_e) with models constructed from 3.8-cm-diameter copper pipes, cut to 30.5-cm lengths and painted to match the approximate reflectivity of a massasauga rattlesnake (Peterson et al. 1993). We placed internal dataloggers (iButton®; Maxim Integrated Products, Sunnyvale, CA), which we programmed to record T_e every hour, within perforated foam blocks at the center of each model, and we sealed pipes with rubber stoppers. To assess the ecological relevance of T_e readings, we evaluated the relationship between T_e and measured body temperatures (T_{IR}) of basking EMRs.

We paired each basking site (i.e., location where we observed a basking EMR) with a nearby random site (sampling approach adapted from Compton et al. [2002]) located along the survey trail and within 25 m of the basking site (a typical daily movement distance for EMRs at Cicero Swamp; Johnson 2000). To minimize bias due to the cut trail at Cicero Swamp, we determined the perpendicular distance of random sites from the survey trail from a normal distribution of mean zero and standard deviation 0.7 m corresponding to the distribution of distances from the trail recorded for EMRs during a 2005 pilot study at Cicero Swamp (K. T. Shoemaker, State University of New York College of Environmental Science and Forestry, unpublished data). We placed environmental temperature thermometers at basking sites and random sites for 2 weeks, starting from the time we initially observed each basking snake. We contrasted T_e between basking sites, paired random sites at time of capture, and averaged for the date of capture with paired sample *t*-tests. Unless otherwise mentioned, we performed all statistical analyses in SAS v.9.0 (SAS Institute, Cary NC); differences associated with $\alpha \leq 0.05$ were interpreted.

Transforming Hourly T_e Data into Metrics of Thermal Quality

Because we deployed T_e thermometers at basking sites for asynchronous 2-week periods, we derived metrics of thermal quality that could be compared directly among basking sites. We built least-squares linear regression models (SAS Institute; PROC REG) to predict hourly T_e at basking sites and random sites for May–September 2006 based on readings from T_e thermometers permanently deployed as reference stations (method adapted from Blouin-Demers and Weatherhead [2002]). We placed reference stations at one open-canopy and one closed-canopy site within each habitat type at Cicero Swamp (5 habitat types × 2 canopy levels = 10 reference stations) and Bergen Swamp (4 habitat types × 2 canopy levels = 8 reference stations). We developed regression equations to predict environmental temperature for each hour of the day (we developed 24 equations for each basking site and random site). We tested predictive ability of these equations by redeploying T_e thermometers at randomly selected basking sites and random sites ($n = 11$) at the end of the field season and evaluating performance metrics (R^2, root mean-square error, mean bias) for observed versus predicted T_e at each site.

For each basking site and random site, we derived 2 comprehensive metrics of thermal quality to which EMRs might reasonably be expected to respond: average daytime T_e (May–Sep) and average number of optimal basking hours/day, defined as the number of hours for which T_e was at or above the lower bound of the thermal set point range (T_{set}) for EMRs (28.4° C, representing the 25% quartile of temperatures selected by EMRs in a laboratory thermal gradient [see below]). Because these 2 metrics were greatly correlated in practice ($r = 0.94$), we used the simplest metric (average daytime T_e) as the primary index of thermal quality. To determine the number of optimal basking hours, we assumed that nearby microhabitats within this heavily vegetated swamp could always readily provide cooler temperatures (shade, below-ground retreat sites) than available at basking sites; therefore, we did not consider an upper bound of T_{set}. We determined the daytime lower bound of T_{set} for EMRs to be 28.4° C in a laboratory study using snakes from the Bruce Peninsula in Ontario, Canada ($n = 14$: 3 gravid, 4 nongravid, 7 M; Harvey 2006). Although T_{set} may differ among source populations, a preference for temperatures of 28° C and above is relatively consistent across temperate snake lineages and we believe is appropriate for EMRs at our study sites (Peterson et al. 1993).

Contrasting Environmental Characteristics at Basking Sites and Random Sites

To relate thermal environment directly to vegetation, we characterized habitat structure for each basking site and random site with 19 habitat measurements: 4 relating to general physiognomy and canopy structure within 5 m of the site, 6 relating to structure and ground cover within a 1-m^2 plot centered on the site, and 9 measured directly at the site (Table 1). We selected many of these variables (e.g., % moss cover, woody-stem density) to facilitate comparison with an earlier EMR habitat selection study at Cicero Swamp (Johnson 1995), whereas we chose other variables (e.g., retreat-site availability, % open-canopy habitat) based on their presumed likelihood to affect temperature or predator avoidance. To measure crypsis potential, we constructed an EMR replica with characteristic size, color, and pattern. We placed this replica at each sampled basking site and random site, and we visually estimated the crypsis of the model on a scale from 0 to 5 (crypsis index; approach adapted from Hanlon et al. [1999]). To train the crypsis index and to validate its ability to predict visibility of EMRs to visual predators, mainly humans and birds of prey, we estimated (on the same scale) the crypsis of all stationary EMRs we encountered. Estimated visibility of an artificial EMR replica (crypsis index) predicted actual snake crypsis ($n = 47$, $R^2 = 0.42$, $P < 0.001$). Therefore, we used the least-squares linear equation describing the relationship (crypsis potential = 1.41 + 0.72 × [crypsis index]) to translate all raw estimates of crypsis index ($n = 96$) into an estimate of crypsis potential for real snakes.

We used Wilcoxon rank-sum tests to evaluate differences between paired basking sites and random sites (Sokal and Rohlf 1981). We also used multiple paired logistic regression in SAS (SAS Institute, PROC LOGISTIC, NOINT option) to evaluate which sets of habitat variables best accounted for observed differences between basking sites and random sites (Hosmer and Lemeshow 1989). We made decisions about which variable combinations to include in the candidate model set a priori, with each candidate model representing a plausible hypothetical basking-site selection pattern (e.g., temp only, temp and low vegetative cover, canopy openness). We excluded some variables (e.g., availability of open-canopy habitat) from candidate models due to correlation (>80%) with similar variables. We did not consider interaction terms due to limited sample size. We selected best model(s) based on small AIC_c (Akaike's Information Criterion; Burnham and Anderson [1998]) and lack of nonsignificant parameters (estimated 95% CI around coeff. must not include zero).

Contrasting Basking-Site Characteristics at Cicero Swamp Versus Bergen Swamp

We assessed thermal characteristics (average daytime T_e, average no. of hr per day at or above T_{set}) and other

Table 1. Environmental variables measured at eastern massasauga rattlesnake basking sites and random sites in Cicero and Bergen Swamps, New York, USA, summer 2006.

Variable	Definition
Within 5-m-radius circle centered on basking site or random site.	
PerOpenCan[a]	Visual estimate of % open-canopy habitat.
PerTrees[a]	Visual estimate of % area with tree cover.
PerShrubs[a]	Visual estimate of % area with shrub cover.
HumClass	Visual estimate of hummock–hollow definition. Scale from 0 (little or no microtopographic resolution) to 4 (knee-high hummocks with wet or mucky hollows).
Within 1-m^2 plot centered at basking site or random site.	
NumWood	Woody-stem density (no. woody stems, mostly shrubs).
PerLitter[a]	Visual estimate of area of ground covered by leaf litter (%).
PerVeg[a]	Visual estimate of area of ground covered by herbaceous vegetation (%).
PerMoss[a]	Visual estimate of area of ground covered by moss (%).
PerSoil[a]	Visual estimate of area of ground covered by bare muck or open water (%; we rarely encountered open water).
CovHtClass	Average ht of woody shrub cover (0–8 [greatest]; classified from measurements of shrub ht).
Measured directly at the basking site or random site.	
CanClass0	Visual estimate of canopy closure at ground level (0–5 [greatest]).
CanClass1	Visual estimate of canopy closure 1 m above ground level (0–5 [highest]).
RetClass	Retreat site availability (0–6 [greatest availability]; classified from measurements of the distance to the nearest visible entrance to a below-ground retreat site).
HumHt	Ht of hummock on which snake/T_e thermometer was located (cm). Measured from lowest elevation point on nearby hollow to the highest elevation on the hummock (not including vegetation).
HumRad	Approximate radius of hummock on which snake/T_e thermometer was located (cm).
DOpenClass	Availability of open-canopy habitat (0–6 [greatest availability]; classified from measurements of the distance to the nearest open-canopy site).
Crypsis	Crypsis of massasauga replica (estimated from 0 to 5 [greatest]).
AvgDayTemp	Average daytime environmental temp during the activity season (° C).
AvgNumHour	Average time at or above optimal T_e/day (no. of hr at or above 28.4° C).

[a] We did not constrain any measured variables to sum to 100%.

environmental characteristics (see Table 1) of basking sites at Cicero Swamp relative to basking sites at Bergen Swamp, which contained extensive open-canopy areas available for basking. We assessed differences between mean basking-site conditions at Cicero Swamp and Bergen Swamp with Mann–Whitney *U*-tests (Sokal and Rohlf 1981). We also characterized environmental temperatures (with the same method as for basking sites and paired random sites) and canopy openness at 9–15 additional sites, which we randomly selected within each habitat type at Cicero Swamp (burn area, upland field, upland forest, red maple swamp, swamp forest) and Bergen Swamp (marl fen, upland field, upland forest, red maple swamp) to evaluate whether thermal differences between basking sites at Cicero Swamp and Bergen Swamp reflected differences in canopy structure and not macroclimatic differences.

Evaluating Management Options

We developed least-squares linear regression models relating vegetation structure (canopy closure and vegetation ht) to basking-site warmth (average daytime T_e) and crypsis potential to explore the potential effects of vegetation management on EMRs at Cicero Swamp. We simulated the response of environmental temperature and crypsis potential to 2 types of habitat manipulation: microhabitat-level (within 1-m^2 plot) reduction of canopy closure and reduction of shrub height (with any other variables remaining constant at mean observed levels). We standardized the units of measurement for both response variables on a scale representing standard deviations from mean basking-site conditions at Bergen Swamp (used as a benchmark) to enable simultaneous consideration of the costs and benefits of management (i.e., improved warmth vs. reduced crypsis potential). Our simulation assumed that 1) the value of basking habitat to snakes is linearly related to environmental temperature and crypsis potential, 2) average basking-site quality (crypsis potential and environmental temp) at Bergen Swamp represents a useful benchmark for restoring basking habitat at Cicero Swamp, and 3) a change of one standard deviation from mean benchmark crypsis potential alters basking-site quality equivalently to a one standard deviation change in mean daytime environmental temperature.

RESULTS

Population Surveys

We identified 38 different basking sites (used by 31 individual snakes) at Cicero Swamp and 10 basking sites (used by 8 individual snakes) at Bergen Swamp. Gravid females accounted for 53% ($n = 20$) of basking observations at Cicero Swamp, and males and nongravid females accounted for 39% ($n = 15$), with the remaining 3 of undetermined sex. Similarly at Bergen Swamp, 50% ($n = 5$) of observed basking sites were selected by gravid females, and 40% ($n = 4$) were selected by males or nongravid females, with the remainder of undetermined sex. As expected, gravid female EMRs were observed basking more frequently than males or nongravid females at Cicero Swamp and Bergen Swamp, assuming a biennial reproductive cycle (Reinert 1981, Seigel 1986), and a 1:1 sex ratio (observed = 52%, expected = 25%, $G_{1,48} = 16.09$, $P < 0.001$; Seigel et al. 1998). Based on 111 snake observations (including nonbasking observations), encounter frequency was greatest during survey hours when ambient temperatures were increasing and least when ambient temperatures were stable or decreasing ($G_{1,111} = 12.23$, df = 1, $P < 0.001$). Compared to Bergen Swamp, a greater proportion of gravid EMR observations at Cicero Swamp consisted of ≥ 2 snakes basking in direct contact (i.e., aggregating) with one another in 2006 and 2007 (17% of 94 observations at Cicero Swamp vs. 0 of 20 observations at Bergen Swamp, Fisher's exact test, $P = 0.036$). Due to few gravid female observations at Bergen Swamp in 2006, we included observations made during the 2007 population surveys. We based all of our other analyses on data collected in 2006. Notably, we observed 6 gravid females climbing shrubs (presumably for basking) at Cicero Swamp in 2006 and 2007, whereas we never observed this behavior at Bergen Swamp.

Response of EMRs to Environmental Temperature Variation

Average T_e at time of capture (29.1° C) was nearly identical to average snake T_{IR} (surface body temp, 29.3° C), indicating that T_e thermometers likely were recording temperatures relevant to basking EMRs. The linear relationship between T_e and T_{IR} was strong ($T_{IR} = 0.32 \times T_e + 19.9$, $R^2 = 0.3$, $P < 0.001$) but flatter than the expected relationship $T_{IR} = T_e$. Thermal inertia, evaporative cooling, physiological adaptations (e.g., blood shunting), and behavioral adjustments (Stevenson 1985) may explain why T_e exhibited greater variance than T_{IR}.

Mean T_e at basking sites at Cicero Swamp ($n = 36$) at time of capture was 5.1° C greater (±6.4° C SD) than at random, paired sites (paired sample *t*-test, $t = 4.7$, df = 35, $P < 0.001$). Averaged over the date of capture, T_e was 2.9° C greater (±2.4° C SD, $t = 7.0$, df = 35, $P < 0.001$) at basking sites than at random sites and was above the lower T_{set} range for EMRs (28.4° C) for an average of 2.1 hours (±2.3 hr SD) longer at basking sites than at random sites ($t = 5.17$, df = 35, $P < 0.001$). At Bergen Swamp ($n = 10$), we detected no temperature difference between basking sites and random sites at time of capture (mean difference = 0.49 ± 5.22° C SD, $t = 0.28$, df = 8, $P = 0.79$) or averaged over the date of capture (mean difference = −0.84 ± 3.39° C SD, $t = -0.75$, df = 8, $P = 0.48$).

Contrasting Environmental Characteristics Between Basking Sites and Random Sites

Based on validation trials from 11 randomly selected basking sites and random sites, our methods for computing environmental temperature outside 2-week T_e thermometer deployment periods (with temp recorded at permanent reference stations) produced relatively accurate and precise hourly T_e estimates: R^2 values for observed versus predicted T_e at individual waypoints averaged 0.98 (±0.01 SD) during initial parameterization ($n = 11$, root mean-square error = 0.82 ± 0.5° C SD), and they averaged 0.91 (±0.07 SD) several months after equations were initially parameterized ($n = 11$, root mean-square error = 1.51 ± 0.95° C SD). Bias was not different from zero during initial parameterization ($\bar{x} = 0.046 \pm 0.085°$ C SD, df = 10, $t = 1.78$, $P = 0.11$) or several months after equations were initially parameterized ($\bar{x} = -0.09 \pm 0.84°$ C SD, df = 10, $t = -0.36$, $P = 0.73$).

Compared with random sites, basking sites at Cicero Swamp generally were warmer, more open-canopy, closer to open microhabitats, and characterized by taller hummocks (Table 2). The paired logistic-regression model that best explained observed differences between basking sites and random sites at Cicero Swamp included only average daytime T_e as a predictor variable (Table 3). A likelihood-ratio test comparing this model to a null model with no predictor variables indicated that the best model fit the data much better than the null model (deviance = 13.32, df = 1, $P \leq 0.001$). Although AIC_c was slightly less for a model including average daytime T_e and crypsis potential, zero was well within the estimated 95% confidence interval around the coefficient for crypsis potential in this model; therefore, there is sparse evidence for including crypsis as an important factor in basking-site selection at Cicero Swamp. At Bergen Swamp, basking sites were closer to retreat sites and had taller hummocks, greater crypsis potential, and greater woody-stem density than random sites (Table 2). Sample size was too small at Bergen Swamp to allow us to build a logistic regression model for basking-site selection.

Contrasting Basking Sites Between Cicero Swamp and Bergen Swamp

Average daytime T_e at EMR basking sites was >2° C (mean difference = 2.5° C) warmer at Bergen Swamp than at Cicero Swamp (Table 4). On average, basking-site T_e at Bergen Swamp was >28.4° C (the lower bound of T_{set} for EMRs) for nearly 1.5 hours longer per day than at Cicero Swamp (Table 4). Basking sites at Bergen Swamp generally had a more open canopy and less shrub cover within a 5-m radius than basking sites at Cicero Swamp (Table 4). Woody cover adjacent to basking sites tended to be shorter at Bergen Swamp than at Cicero Swamp (Table 4).

Habitat types at Bergen Swamp and Cicero Swamp with similar vegetation also were thermally similar, suggesting no substantial macroclimate differences between Bergen Swamp and Cicero Swamp (Fig. 1); mean environmental temperature did not differ between red maple swamp habitats (mean difference = 0.12° C, $t = 0.24$, df = 26, $P = 0.821$) or upland forest habitats (mean difference = 0.16° C, $t = 0.40$, df = 20, $P = 0.73$) at the 2 sites. Observed thermal differences between primary EMR habitat at Bergen Swamp and Cicero Swamp (burn area and marl fen; mean difference = 2.85° C, $t = 3.10$, df = 28, $P = 0.009$) and between basking sites at Bergen Swamp and Cicero Swamp (Table 4) closely tracked differences in mean percent canopy openness (Pearson's $r = 0.72$; Fig. 1).

Relating Basking-Site Quality (T_e and Crypsis Potential) to Microhabitat Structure

Vegetation management at Cicero Swamp was simulated with the following least-squares linear regression models: average daytime environmental temperature = 25.2 − 1.2 ×

Table 2. Contrasting eastern massasauga rattlesnake (EMR) basking sites with paired random sites in New York, USA, based on data from June to August 2006. Median and inter-quartile range (IQR) of paired differences indicate central tendency and dispersion, respectively. We derived *P*-values from Wilcoxon rank-sum tests (H_0: difference = 0). Positive differences indicate values were greater at basking sites. Except where noted df = 37 for Cicero Swamp and df = 9 for Bergen Swamp.

	Cicero Swamp (*n* = 38)			Bergen Swamp (*n* = 10)		
Variable[a]	**Median**	**IQR**	***P***	**Median**	**IQR**	***P***
CanClass0	−1	−2–0	<0.001	0.50	0–1	0.359
CanClass1	0	−1–0	0.067	0	0–0	0.5
RetClass	0	−1–1	0.506	1	1–2	0.007
HumHt	0.01	−0.04–0.17	0.025	0.15	0.1–0.2	0.004
HumRad	0	−0.55–0.30	0.264	0.27	−0.03–0.65	0.250
DOpenClass	1.5	0–2	<0.001	0	0–0	1.0
Crypsis	0	−0.72–0.72	0.798	0.54	0–0.93	0.016
NumWood	6	−14–19	0.317	10	5–21	0.006
PerLitter	5	−7–20	0.077	2.5	−5–15	0.312
PerVeg	0	−5–5	0.885	0.5	−15–10	0.605
PerMoss	−7	−22–5	0.058	0	−15–15	0.773
PerSoil	0	−5–5	0.748	5	−10–12	0.621
CovHtClass	0	−1–2	0.243	0	0–0	0.625
AvgDayTemp[b]	2.20	1.16–3.15	<0.001	0.55	−1.92–1.48	0.921
AvgNumHour[b]	1.59	0.46–2.61	<0.001	0.46	−1.19–1.19	0.572

[a] CanClass0 = canopy closure at ground level (0–5); CanClass1 = canopy closure 1 m above ground level (0–5); RetClass = retreat site availability (0–6, classified from distance to nearest retreat site); HumHt = ht (cm) of hummock on which T_e thermometer was located; HumRad = radius (cm) of hummock on which T_e thermometer was located; DOpenClass = availability of open-canopy habitat (0–6, classified from distance to nearest open-canopy site); Crypsis = crypsis potential (0–5, estimated from visibility of EMR replica); NumWood = woody-stem density within 1-m^2 plot; PerLitter = % ground area in 1-m^2 plot covered by leaf litter; PerVeg = % ground area in 1-m^2 plot covered by herbaceous vegetation; PerMoss = % ground area in 1-m^2 plot covered by moss; PerSoil = % ground area in 1-m^2 plot covered by muck, soil, or open water; CovHtClass = average ht of woody shrub cover in 1-m^2 plot (0–8, classified from measurements of shrub ht); AvgDayTemp = average daytime environmental temp (° C) during the activity season; AvgNumHour = average time (hr) at or above optimal T_e/day.

[b] Due to T_e thermometer failures, df for thermal metrics was reduced at Cicero Swamp (df = 35) and Bergen Swamp (df = 8).

(canopy closure at ground level) − 0.28 × (average ht of woody shrub cover); crypsis potential = 2.0 + 0.28 × (canopy closure at ground level). Our simulations indicated that management of canopy closure and shrub height may be necessary to create viable basking habitat at Cicero Swamp. With shrub height held constant at mean levels observed within the burn area at Cicero Swamp (2.0 m, based on 16 random locations), 95% confidence regions for warmth and crypsis potential failed to intersect substantially for any simulated canopy-closure treatment (Fig. 2a). Alternatively, canopy thinning coupled with reduction in shrub height (shrub ht reduced to 0.5 m, a ht typical for the marl fen at Bergen Swamp) produced a substantial intersection region that more closely approximated (but still generally fell short of) mean basking conditions at Bergen Swamp (Fig. 2b). An intersection region that more closely approximates benchmark conditions may be achieved by shifting the temperature curve upward on the y-axis while holding the crypsis curve at current levels (Fig. 2c), a solution we hypothesize could be achieved by reducing shrub height beyond the 1-m^2 scale investigated.

DISCUSSION

Our evaluation of the thermal limitation hypothesis indicates encroachment of tall shrubs is limiting opportunities for snake thermoregulation at Cicero Swamp, where EMRs chose basking sites primarily based on greater environmental temperature relative to randomly selected sites. In contrast, EMRs at Bergen Swamp, where open-canopy basking sites are abundant, may select basking sites

Table 3. Comparison of the best candidate models (paired logistic regression) explaining differences (*n* = 36) between eastern massasauga rattlesnake (EMR) basking sites and paired sites at Cicero Swamp, New York, USA, based on data from June to August 2006.

Variables included[a]	**Pseudo R^2**	**Log likelihood**	**K**[b]	**AIC_c**[c]	**Δ_i**[d]	**Akaike wt**[e]
AvgDayTemp, Crypsis	0.64	−6.80	3	18.3	0.00	0.53
AvgDayTemp	0.60	−8.34	2	19.0	0.69	0.37
AvgDayTemp, Canclass0	0.60	−8.34	3	21.4	3.07	0.11
AvgDayTemp, NumWood, CovHtClass	0.62	−7.65	4	22.6	4.23	0.06
AvgDayTemp, HumHt, RetClass	0.61	−8.08	4	23.4	5.09	0.04
CanClass0	0.35	−17.2	2	36.8	18.51	0.00

[a] CanClass0 = canopy closure at ground level (0–5); RetClass = retreat site availability (0–6, classified from distance to nearest retreat site); HumHt = ht (cm) of hummock on which T_e thermometer was located; Crypsis = crypsis potential (0–5, estimated from visibility of EMR replica); NumWood = woody-stem density within 1-m^2 plot; CovHtClass = average ht of woody shrub cover in 1-m^2 plot (0–8, classified from measurements of shrub ht); AvgDayTemp = average daytime environmental temp (° C) during the activity season.

[b] K = the no. of estimable parameters in the model.

[c] AIC_c = Akaike's Information Criterion, corrected for small sample size.

[d] Δ_i = difference between model AIC_c and AIC_c for the best model in the set.

[e] Akaike wt = estimate of relative model strength.

Table 4. Contrasting eastern massasauga rattlesnake (EMR) basking sites at Bergen Swamp and at Cicero Swamp, New York, USA, based on data from June to August 2006. Median and inter-quartile range (IQR) indicate central tendency and dispersion, respectively. We derived *P*-values from Mann–Whitney *U*-tests (H_0: difference = 0). Except where otherwise noted, df = 46 for all tests.

	Bergen ($n = 10$)		Cicero ($n = 38$)		
Variable[a]	**Median**	**IQR**	**Median**	**IQR**	***P***
PerOpenCan	85	80–90	14	9–25	<0.001
HumClass	3	2–3	3.0	2–4	0.184
PerTrees	5	5–20	8	5–10	0.938
PerShrubs	20	10–35	90	80–92	<0.001
CanClass0	1	1–2	2.0	1–3	0.038
CanClass1	0	0–0	1	0–2	0.009
RetClass	4	4–5	5	4–6	0.190
HumHt	0.3	0.2–0.35	0.3	0.15–0.35	0.750
Crypsis	3.02	2.63–4.28	3.2	2.48–4.28	0.928
NumWood	16.5	10–24	36.5	16–55	0.043
PerLitter	37.5	20–65	65	30–79	0.105
PerVeg	55	15–75	10	7–15	0.002
PerMoss	1	10–25	25	10–60	0.146
PerSoil	20	5–25	5	0–10	0.020
CovHtClass	8	7–8	5	4–6	<0.001
AvgDayTemp[b]	27.2	26.1–28.0	23.7	22.4–25.7	0.001
AvgNumHours[b]	8.08	6.63–8.49	6.33	5.5–7.2	0.010

[a] PerOpenCan = % open-canopy habitat within 5-m-radius circle; HumClass = visual estimate of hummock–hollow definition within 5-m-radius circle; PerTrees = % area with tree cover within 5-m-radius circle; PerShrubs = % area with shrub cover within 5-m-radius circle; CanClass0 = canopy closure at ground level (0–5); CanClass1 = canopy closure 1 m above ground level (0–5); RetClass = retreat site availability (0–6, classified from distance to nearest retreat site); HumHt = ht (cm) of hummock on which T_e thermometer was located; Crypsis = crypsis potential (0–5, estimated from visibility of EMR replica); NumWood = woody-stem density within 1-m^2 plot; PerLitter = % ground area in 1-m^2 plot covered by leaf litter; PerVeg = % ground area in 1-m^2 plot covered by herbaceous vegetation; PerMoss = % ground area in 1-m^2 plot covered by moss; PerSoil = % ground area in 1-m^2 plot covered by muck, soil, or open water; CovHtClass = average ht of woody shrub cover in 1-m^2 plot (0–8, classified from measurements of shrub ht); AvgDayTemp = average daytime environmental temp (° C) during the activity season; AvgNumHour = average time (hr) at or above optimal T_e/day.

[b] Due to iButton failures, df for thermal metrics was reduced to 44.

based on relative crypsis potential and, hence, protection from predators. Our findings suggest that both warmth and crypsis potential are key determinants of basking-site quality for EMRs.

Mean body temperature differences of the magnitude we observed between basking sites at Bergen Swamp and Cicero Swamp (>2° C) may substantially improve offspring viability (O'Donnell and Arnold 2005). In addition, studies of garter snake (*Thamnophis* spp.) thermal biology have shown that an average difference of 1.0° C during gestation can alter gestation time by 5–8 days (Peterson et al. 1993). By shortening the gestation period, vegetation management may increase the likelihood that both mother and offspring find food and a suitable hibernaculum before winter.

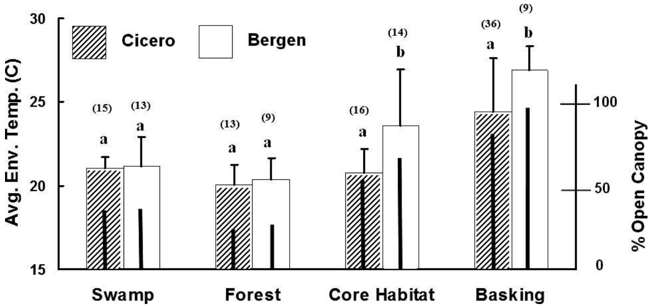

Figure 1. Contrasting average environmental temperature (Avg. Env. Temp.) by habitat type for eastern massasauga rattlesnakes at Cicero Swamp and Bergen Swamp, New York, USA, based on data from June to August 2006. Wide bars labeled Swamp, Forest, and Core Habitat (burn area at Cicero Swamp and marl fen at Bergen Swamp) represent mean daytime environmental temperature for eastern massasauga rattlesnakes (T_e, left vertical axis) within these respective habitat types (no. in parentheses indicate sample size). Wide bar labeled Basking represents mean daytime T_e recorded at known eastern massasauga rattlesnake basking sites. Error bars represent one standard deviation from the mean. Means labeled with the same letter are not different at $\alpha = 0.05$. Solid bars within the wide bars indicate mean canopy openness (right axis). Habitat-specific T_e differences between Cicero Swamp and Bergen Swamp closely track differences in mean canopy openness, suggesting that thermal differences at basking sites between Cicero Swamp and Bergen Swamp reflect vegetation, not macroclimate, differences.

Snakes likely require ready access to a wide thermal gradient to thermoregulate effectively (Spellerberg 1975, 1988). We encountered basking snakes more often than expected during survey hours when environmental temperatures were increasing, indicating that basking sites in our study were used by EMRs primarily to increase body temperatures rather than to maintain high body temperatures. Once snakes achieved optimal core temperatures at their warming sites, we suspect they retreated into more cryptic microhabitats where they were less amenable to visual detection. Cryptic basking behavior (see Nilson et al. 1999), in which snakes thermoregulate under conditions of minimal exposure (e.g., partially engulfed within natural crevices or hidden beneath dense ground cover) was likely underrepresented in our study due to our reliance on visual-encounter surveys. Microhabitats providing thermally suitable retreat sites or cryptic cover may be an important constituent of high-quality basking habitat, especially when interspersed with warming sites such as those we characterized. Controlled mesocosm experiments (e.g., Mullin and Gutzke 1999) would better distinguish the specific roles of temperature and crypsis in basking-habitat selection by

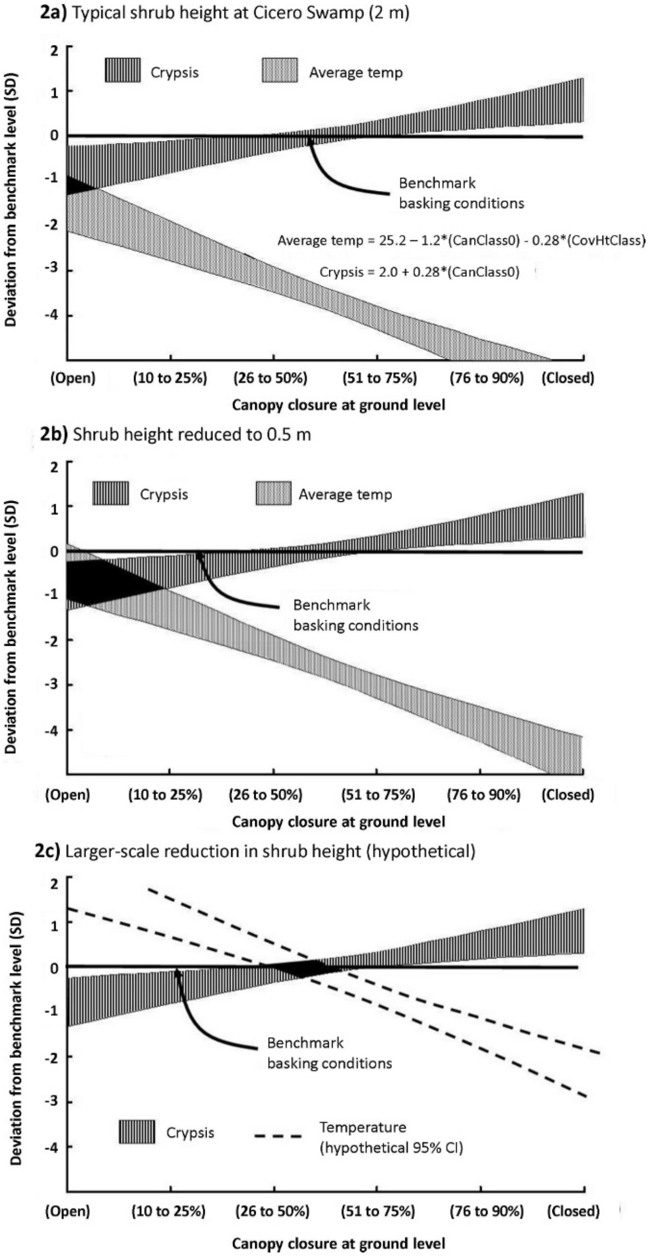

Figure 2. Simulated habitat management for eastern massasauga rattlesnakes (EMR) at Cicero Swamp, New York, USA. Average basking-site temperature (average daytime environmental temp [° C] during the activity season) and crypsis potential (estimated from 0 to 5 based on visibility of an EMR replica) are displayed as standard deviations from mean (benchmark) values recorded at Bergen Swamp, New York. Both response variables are modeled as linear functions of canopy closure (CanClass0; canopy closure at ground level, classified from 0 to 5) and shrub height (CovHtClass; average ht of woody shrub cover in 1-m^2 plot, classified from 0 to 8 based on measured shrub hts) based on data collected from June to August 2006. Shaded areas represent 95% confidence intervals around mean predicted values, with intersection regions indicating optimal management solutions. a) Creation of canopy gaps alone may be an insufficient management strategy at Cicero Swamp, because there is no substantial intersection region. b) Reducing shrub height within created canopy gaps improves the optimal management solution; however, the intersection region still falls short of benchmark basking conditions defined by the difference from reference level = 0° C. c) We hypothesize that a management solution closely approximating benchmark conditions may be possible via larger scale (beyond the 1-m^2 microhabitat scale) reduction of shrub height.

snakes. Reptiles like the EMR may possess mechanisms for optimizing the conflicting demands of warmth and crypsis, the knowledge of which would assist stakeholders in setting informed vegetation management targets.

Our management simulation models (Fig. 2a, b) suggest that vegetation management at the microhabitat level, which we defined as 1 m^2, is not a viable management solution. Even the most promising microhabitat-level management solution for Cicero Swamp (substantial reduction of canopy cover and shrub ht) produced simulated basking conditions less suitable in terms of warmth and crypsis than those observed at Bergen Swamp. Considering that basking sites at Cicero Swamp were generally located <5 m from tall (≥ 2 m) shrubs or trees, whereas those at Bergen Swamp were embedded within large open-canopy areas, we hypothesize that management at larger spatial scales may be required (Fig. 2c). However, to reduce unnecessary habitat disruption and financial burden, we caution that vegetation management should proceed at the smallest scale necessary to achieve the desired thermoregulatory benefits.

To develop management recommendations for Cicero Swamp, we assume that basking sites selected by EMRs at Bergen Swamp represent a useful benchmark for restoring basking habitat at Cicero Swamp. We do not claim that basking-site conditions at Bergen Swamp represented a true optimum for EMRs or that overall habitat conditions were superior at Bergen Swamp. If anything, small sample size at Bergen Swamp (in addition to unpublished 2007 capture–recapture evidence) suggests that EMR abundance may be lower at this site. In addition, sample size was very small at Bergen Swamp (10 basking sites used by 8 individual snakes), limiting the precision of our estimates of benchmark conditions. Setting aside the question of what habitat factors may limit EMR abundance at Bergen Swamp (a question on which we can only speculate) our results support the hypothesis that quality of basking habitat is greater at Bergen Swamp.

With a clear problem, a promising management solution, and tractable means of evaluating success (e.g., frequency of use, gestation time), management of basking habitat at Cicero Swamp and similar overgrown snake habitats represents an excellent opportunity to pursue an evidence-based approach to snake conservation (e.g., Smallwood et al. 1999, Pullin and Knight 2005, Nichols and Williams 2006). Manipulation of variables such as canopy-gap size and ground-cover heterogeneity within experimental treatments would assist stakeholders in developing effective management strategies for thermally limited reptiles. Indirect indicators of habitat quality, such as those measured in our study (e.g., environmental temp, crypsis, and habitat selection) can be used to monitor the success of habitat manipulation, ideally along with direct indicators of population viability such as population trends, gestation time, survival rates, and number of viable offspring (e.g., Seigel et al. 1998).

MANAGEMENT IMPLICATIONS

We conclude that brush clearing is likely to enhance thermoregulation potential at Cicero Swamp and that EMRs are likely to respond favorably to management aimed at improving basking habitat. Vegetation management may be warranted to improve the conservation status of EMRs and other reptiles faced with thermal limitation, presumably by allowing snakes to achieve greater body temperatures for longer periods (i.e., to thermoregulate more effectively) and to avoid increased predation risk associated with extensive thermoregulatory movements and prolonged periods of exposure. We hypothesize that canopy-gap size, heterogeneity of vegetative cover, and retreat-site availability are important determinants of basking-site quality that should be considered in setting management targets. We propose the creation of experimental management plots ranging from 10 m^2 to 100 m^2, with shrub height reduced to 0.25–0.5 m in each treatment plot. Reduction in shrub height over these spatial scales should provide a natural interspersion of warming sites (edges of shrub hummocks) and cryptic basking sites (center of hummocks), while minimizing unintended negative side effects (e.g., degradation of habitat required for foraging or hibernation).

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