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# THE INFLUENCE OF REPRODUCTIVE STATUS ON THERMAL ECOLOGY AND VEGETATION USE OF FEMALE EASTERN MASSASAUGA RATTLESNAKES (*SISTRURUS CATENATUS CATENATUS*) IN SOUTHWESTERN MICHIGAN

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**Abstract.**—The Eastern Massasauga (*Sistrurus catenatus catenatus*) is a viviparous rattlesnake that is a species of “special concern” in Michigan and listed as state-threatened or endangered throughout the rest of its range. Viviparous species typically have unique thermal needs associated with the internal development of young, and these needs can influence vegetation selection patterns. We investigated the thermal ecology and vegetation selection of female *S. c. catenatus*. We radio-tracked eight gravid and six non-gravid female *S. c. catenatus* implanted with temperature-sensitive transmitters in southwestern Michigan during May–August 2004 and 2005. Gravid *S. c. catenatus* generally maintained higher average body temperature ( $T_b$ ; 29.1–34.1°C) throughout the season than non-gravid females (22.2–30.8°C), and also maintained plateau temperatures longer in the diel cycle. Gravid females maintained significantly higher ( $P < 0.01$ ) mean temperatures above ambient compared with non-gravids early (i.e., May; gravid = 11.7°C; non-gravid = 6.1°C) and late (i.e., July and August; gravid = 7.1°C; non-gravid = 4.9°C) in the season. These results suggest gravid females were thermoregulating to facilitate embryogenesis. Gravid *S. c. catenatus* selected early/mid-successional deciduous upland vegetation, and these areas had significantly higher ( $P < 0.001$ ) mean soil temperatures (19.9°C) than early/mid-successional wetlands (17.4°C). Therefore, we recommend that upland areas adjacent to wetlands supporting *S. c. catenatus* be maintained in early successional vegetation types with limited woody encroachment. This vegetation type provides gravid females with favorable thermal conditions to meet their reproductive requirements.

**Key Words.**—habitat use; Massasauga; rattlesnake; reproduction; *Sistrurus*; thermal ecology; thermoregulation; vegetation;

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## INTRODUCTION

The Eastern Massasauga (*Sistrurus catenatus catenatus*; Fig. 1) was once common throughout the lower Great Lakes basin. Today, *S. c. catenatus* is a species of “special concern” in Michigan and is listed as state-threatened or endangered throughout the rest of its range. Hypothesized mechanisms for the decline of *S. c. catenatus* include habitat fragmentation and degradation (Harding 1997). In particular, there have been high rates of historic wetland loss in the conterminous United States (i.e., > 50%; Dahl, T. E. 1990. Wetlands losses in the United States, 1780s to 1980s. United States Fish and Wildlife Service, unpubl. report. 21 p.) that have negatively impacted *S. c. catenatus* populations (Seigel 1986). Additionally, adjacent uplands used by *S. c. catenatus* are not regulated by federal and most state laws. The destruction or development of these areas

may be contributing to continued population declines (Szymanski, J. 1998. Status assessment for Eastern Massasauga [*Sistrurus c. catenatus*]. United States Fish and Wildlife Service, Endangered Species Division. unpubl. report. 30 p.).

As a viviparous species, *S. c. catenatus* has unique life-history patterns associated with the internal development of young. Viviparity confers benefits to the developing embryos, including protection and investment of nutrients during gestation (Dmiel 1970; Shine and Bull 1979). Most importantly, behavioral thermoregulation allows viviparous species to control the thermal environment of developing embryos (Blanchard and Blanchard 1941; Andrews and Mathies 2000). Gravid females can provide embryos with a warmer microenvironment, thereby speeding development (Blanchard and Blanchard 1941). This is particularly important in temperate regions, where cold



**FIGURE 1.** The Eastern Massasauga (*Sistrurus catenatus catenatus*) from the Pierce Cedar Creek Institute in Hastings, Michigan, USA. (Photographed by Kristin Bissell)

conditions might slow development and prevent birth prior to winter (Shine and Bull 1979).

While beneficial to offspring, viviparity is costly to adult females. Gravid females typically exhibit reduced food intake leading to anorexia prior to parturition and, therefore, have limited energy resources (Gregory et al. 1999; Gignac and Gregory 2005). These energetic constraints result in a trade-off in thermal optima whereby gravid females should reduce body temperature ( $T_b$ ) to conserve energy and embryos require increased  $T_b$  for development (Beuchat and Ellner 1987). This thermal conflict is resolved in different ways by different species. Some species increase  $T_b$  during pregnancy (e.g., *Crotalus viridis viridis*; Graves and Duvall 1993); whereas, others do not raise  $T_b$  (e.g., *Agkistrodon contortrix*; Sanders and Jacob 1981). The thermal ecology of *S. c. catenatus* during pregnancy has not been reported.

Vegetation use can influence the thermal patterns of snakes because it provides cover and basking opportunities thereby allowing snakes to behaviorally raise or lower  $T_b$ . Gravid females that have different needs (e.g., foraging, thermal) and constraints (e.g., energetic) may use different vegetation types compared with non-gravid females (Charland and Gregory 1995).

Specifically, gravid females with high optimal  $T_b$  should select vegetation types that maximize basking opportunities (Charland and Gregory 1995). *Sistrurus c. catenatus* uses a variety of wetland vegetation types and associated uplands throughout its range (Szymanski. 1998. *op. cit.*). Although Reinart and Kodrich (1982) noted that gravid females chose locations with higher maximum daily temperatures compared with non-gravid females, no general patterns have emerged with respect to vegetation selection by gravid females (Szymanski. 1998. *op. cit.*).

The thermal requirements of gravid *S. c. catenatus* and the influence of reproductive status on vegetation selection patterns remain poorly understood. Thus, our objectives were to: (1) quantify differences in the thermal ecology between gravid and non-gravid female *S. c. catenatus* in southwestern Michigan; (2) quantify vegetation selection patterns of gravid and non-gravid female *S. c. catenatus*; and (3) quantify the thermal properties of vegetation types used by *S. c. catenatus*. This information will provide a better understanding of the environmental components necessary for the reproductive success of *S. c. catenatus*, and will help guide conservation efforts.

**MATERIALS AND METHODS**

Our study was conducted in Barry County in southwestern Michigan, USA, at the Pierce Cedar Creek Institute for Ecological Education (PCCI) in 2004 and 2005 and was expanded to include the Yankee Springs State Recreation Area (YSRA) in 2005. PCCI is approximately 300 ha of privately owned property managed as a preserve and YSRA is approximately 2,100 ha managed by the Michigan Department of Natural Resources (MDNR). We searched for and captured 12 female *S. c. catenatus* during mid-April to early August in wetlands and adjacent uplands at PCCI (seven gravids and five non-gravids) and captured two females at YSRA (one gravid and one non-gravid).

We devised an ecological classification system (ECS; Table 1) to classify vegetation types occupied by *S. c. catenatus* on a daily basis. This ECS takes into account the hydrological, geological, and successional attributes

**TABLE 1.** Ecological classification system used to classify vegetation stands occupied by *Sistrurus c. catenatus* on a daily basis, and percentage cover of each vegetation class in the legal sections comprising the Pierce Cedar Creek Institute (PCCI) and Yankee Springs State Recreation Area (YSRA) study sites in Michigan, USA. Successional stage was generalized as early to mid-successional (E/M) or late successional (L) for all subclasses except water and developed.

Study Site	Succession	Fen		Sedge/Forb Wetland		Water	Grass/Forb		Developed
		Herbaceous	Scrub-shrub	Deciduous	Coniferous		Deciduous	Coniferous	
PCCI	E/M	0	0	21.6	0	2.3	30.8	0	1.9
	L	0	0	8.3	2.5		27.5	5.1	
YSRA	E/M	0	5.0	2.0	0	8.3	12.0	0	0.9
	L	0	0	2.6	0.3		57.4	11.5	

of the vegetation, while generalizing vegetation to deciduous or coniferous based on the dominant overstory species present. We defined available vegetation as the percentage coverage of each vegetation class in the legal section(s) comprising the study areas (i.e., T02N, R08W, sections 19 and 30 for PCCI, and T03N, R10W, section 27 for YSRA; Bissell 2006). Vegetation at PCCI consisted primarily of late successional uplands (33%), early successional uplands (31%) and early successional wetlands (22%), whereas vegetation at YSRA was dominated by late successional uplands (69%) with less than 20% cumulative coverage of early-successional vegetation (Table 1).

Captured snakes were taken immediately to Potter Park Zoo Veterinary Clinic in Lansing, Michigan, and were surgically implanted with temperature-sensitive 5-g transmitters (SB-2T, Holohil Systems Ltd., Carp, Ontario, Canada). Transmitters were implanted following procedures outlined by Reinart and Cundall (1982) and Weatherhead and Anderka (1984) modified by B. Kingsbury (Indiana-Purdue University at Fort Wayne) and T. Harrison (Potter Park Zoo; Bissell 2006). Transmitters did not have a mass > 5% of a snake's body mass (Samuel and Fuller 1996; Parent and Weatherhead 2000). Snakes were allowed to recover from surgery in captivity for approximately three days prior to release at their point of capture.

We located each snake once daily (time of location for each individual varied among days), at which time we recorded their location, transmitter pulse rate (used to calculate  $T_b$ ), and ambient and nearby (i.e., < 3 m) soil temperatures. We included data from the date of release following telemeter implantation until parturition for gravid females, and for non-gravid females, from the date of release until August 17 (the mean parturition date [MPD] for all gravid females in this study). We excluded data points after parturition because thermal optima and vegetation selection patterns were expected to change following parturition, when females are no longer constrained thermally or physically by embryos (Derickson 1976; Gregory et al. 1999).

The temperature-sensitive transmitters were factory calibrated by Holohil Systems, Ltd. We used cubic regression models (PROC NLIN; SAS Institute Incorporated, Cary, North Carolina, USA) to relate pulse interval to  $T_b$  using the calibration points. These models explained significant variation in  $T_b$  ( $r^2 > 0.99$ ) at initial calibration, but are not presented herein because each model was specific to an individual transmitter.

We recovered transmitters from one male snake (not included in this study) and one post-parturition gravid female (included in the study) that were lost to predation; as well as, a non-gravid female (not included in this study) that was lost to health complications (Bissell 2006). Recovered transmitters were recalibrated in a water bath following snake mortality to

assess drift (i.e., changes in the relationship between transmitter pulse interval and temperature following initial calibration), which was assumed to be constant over time. We multiplied the resulting daily drift correction ( $0.38 \text{ milliseconds pulse}^{-1}$ ,  $SE = 0.04 \text{ milliseconds pulse}^{-1}$ ) by the number of days following telemeter activation and added the result to each pulse rate. This drift-corrected pulse rate was used to generate  $T_b$  estimates from the unique cubic function for each transmitter.

We used a four-way repeated-measures analysis-of-variance (ANOVA) to simultaneously test for differences in  $T_b$  between two reproductive classes (gravid and non-gravid), among six season categories (12–31 May, 1–15 June, 16–30 June, 1–15 July, 16–31 July, and 1 August through parturition or MPD), four time categories (0000–0559, 0600–1159, 1200–1759 and 1800–1159), and between two years of study (2004 and 2005; PROC MIXED, SAS Institute Incorporated, Cary, North Carolina, USA). We included reproductive class by season, time and year category interaction terms in the repeated-measures ANOVA and performed analyses by reproductive class when the interaction was significant. We performed an identical ANOVA for the difference between  $T_b$  and ambient temperature (i.e.,  $T_b - T_a$ ), except that we did not include time category or reproductive class by time category terms in the model.

We used one-way ANOVA to test for differences in ambient temperature between years and to test for differences in soil temperature between early/mid-successional deciduous wetlands and early/mid-successional deciduous uplands at PCCI. When ANOVA indicated that effects were significant, we made pairwise comparisons using Tukey's Honestly Significant Difference (HSD) multiple comparison test. All analyses were conducted using the SAS® system at  $\alpha = 0.05$ .

We qualitatively compared mean  $T_b$  of gravid and non-gravid *S. c. catenatus* and soil temperatures at snake locations between YSRA and PCCI in 2005, but did not run statistical tests because of low sample size at YSRA. We plotted mean  $T_b$  for each 2-h period throughout the day to qualitatively compare diel thermal patterns of gravid and non-gravid  $T_b$ . Finally, we used a chi-square test for association ( $\alpha = 0.05$ ) to test for differences in vegetation class selection between gravid and non-gravid females at PCCI. We did not run statistical tests on vegetation use at YSRA because of small sample size.

## RESULTS

Reproductive status and season category interacted for  $T_b$  and  $T_b - T_a$  ( $F_{5,41} > 2.94$ ,  $P < 0.02$ ). Mean  $T_b$  of gravid female *S. c. catenatus* was significantly higher than non-gravid females in three of six season categories (see Table 2). Similarly, mean  $T_b - T_a$  of gravid female *S. c.*

**TABLE 2.** Mean body temperature ( $T_b$  [°C]) and difference from ambient temperature ( $T_b - T_a$  [°C]) of gravid and non-gravid female *Sistrurus c. catenatus* between late May and August in southwestern Michigan, USA. Means within columns followed by unlike letters are statistically different by repeated-measures ANOVA and Tukey's Honestly Significant Difference test. Paired means within rows followed by asterisks (\*) or triangles (▲) are statistically different between reproductive classes by ANOVA.

Date	Reproductive Class							
	Gravid				Non-gravid			
	<i>n</i>	$T_b$	SE	$T_b - T_a$	<i>n</i>	$T_b$	SE	$T_b - T_a$
12-31 May	3	34.12 a*	0.46	11.67 a▲	1	22.16 a	1.08	6.14 a
1-15 June	4	31.36 ab	0.73	5.22 b	3	30.82 b	1.34	5.34 a
16-30 June	7	29.74 b	0.67	7.32 b	5	27.86 bc	0.94	6.36 a
1-15 July	8	29.05 b*	0.56	6.90 b▲	6	26.72 c	0.63	4.68 a
15-31 July	8	30.25 ab*	0.46	7.63 b▲	6	27.91 bc	0.57	5.04 a
August <sup>†</sup>	8	29.97 b	0.45	6.82 b▲	6	29.04 bc	0.48	5.10 a

<sup>†</sup> Includes data from 1 August through parturition for gravid females and 1 August through the mean parturition date (17 August) for non-gravid females.

*catenatus* was significantly higher in four of six season categories. Gravid female  $T_b$ s were highest, and non-gravid  $T_b$  was lowest, for the 12–31 May time period. Gravid females maintained mean  $T_b$ s up to 11.67°C above ambient temperature, which was nearly two times higher than the maximum for non-gravid females (6.36°C; Table 2). Mean  $T_b$  was similar between sites in 2005, with gravid females averaging 31.73°C (SE = 0.31) at PCCI and 31.02°C (SE = 0.69) at YSRA. Mean  $T_b$  for non-gravid females in 2005 was 28.71°C (SE = 0.46) at PCCI and 28.53°C (SE = 0.86) at YSRA.

Body temperature differed among time categories ( $F_{3,33} = 103.41$ ,  $P < 0.001$ ). Tukey's HSD showed that  $T_b$ s were significantly lowest during the 0000–0559 time period (21.35°C, SE = 0.75), intermediate during the 0600–1159 and 1800–2359 time periods (27.35°C, SE = 0.24), and significantly highest during the 1200–1759 time period (32.38°C, SE = 0.22). Gravid females tended to reach peak temperature earlier in the day and maintained this peak longer and with less variability in plateau temperatures (*sensu* Peterson 1987) than non-gravid females (Fig. 2). Finally,  $T_b$ ,  $T_b - T_a$ , and  $T_a$  differed between years ( $F_{1,10} > 10.88$ ,  $P < 0.01$ ), with mean  $T_b$  in 2004 (27.49°C, SE = 0.29) significantly lower than 2005 (30.33°C, SE = 0.29). Conversely,  $T_b - T_a$  was significantly greater in 2004 (7.30°C, SE = 0.19) than 2005 (5.43°C, SE = 0.18). Mean  $T_a$  in 2004 (20.20°C, SE = 0.25) was significantly lower than 2005 (24.95°C, SE = 0.26).

*Sistrurus c. catenatus* at PCCI used early/mid-successional deciduous uplands (representing 30.8% of available cover) and early/mid-successional deciduous wetlands (21.6%) within PCCI, almost exclusively (Table 1, Fig. 3). One individual was located twice in the late successional coniferous wetland vegetation type, which represented 2.5% of available cover (Table 1, Fig. 3). Reproductive status significantly influenced vegetation selection by individuals at PCCI ( $\chi^2 = 53.1$ ,  $P < 0.001$ ), with gravid females choosing early/mid-successional upland vegetation more often than non-gravid females. Early/mid-successional deciduous

wetlands and uplands were accessible to all *S. c. catenatus* on the study area because every snake in the study hibernated near the wetland/upland ecotone (Bissell 2006). Soil temperature was significantly greater ( $F_{1,732} = 23.26$ ,  $P < 0.001$ ) for location events in early/mid-successional deciduous uplands (19.93°C, SE = 0.19) than early/mid-successional deciduous wetlands (17.35°C, SE = 0.13). At YSRA, 100% of locations for the two snakes in the study were classified as early/mid-successional scrub-shrub fen, which represented 5.0% of the available cover within the legal section. Soil temperatures in 2005 were similar between PCCI (20.01°C, SE = 0.19) and YSRA (20.08°C, SE = 0.22).

## DISCUSSION

Gravid *S. c. catenatus* generally maintained higher  $T_b$  than non-gravid females. This is consistent with other temperate viviparous species such as *Crotalus viridis* (Gier et al 1989; Charland and Gregory 1990) and *Nerodia rhombifera* (Tu and Hutchinson 1994). Gravid female *S. c. catenatus* likely reduce feeding during gestation (Gignac and Gregory 2005), and the majority of females at PCCI do not have sufficient reserves to reproduce annually (Bissell 2006). Thus, gravid females are limited energetically and should have lower thermal optima than non-gravid females to slow metabolism and energy expenditure (Beuchat and Ellner 1987). The maintenance of higher  $T_b$ s, hence higher metabolic rates, by gravid females suggests the thermal optima of developing embryos is greater than that of adult females (Beuchat and Ellner 1987).

Non-gravid female *S. c. catenatus* tended to reach peak  $T_b$  almost an hour later in the diel thermal cycle and started reducing  $T_b$  an hour earlier than gravid females. Additionally, variability in gravid female  $T_b$  during the plateau phase was less pronounced, which suggests gravid females are more constrained by the thermal and metabolic needs of embryos. Presumably, non-gravid females can lower  $T_b$  to limit metabolic expenditure when energy is limiting (e.g., in times of low prey

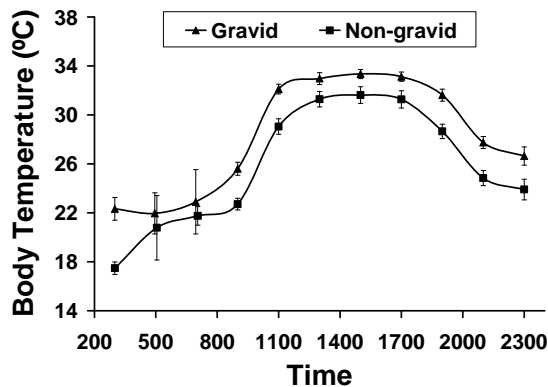


FIGURE 2. Mean  $T_b$  of telemetered gravid ( $n = 8$ ) and non-gravid ( $n = 6$ ) female *Sistrurus c. catenatus* for each 2h period between 0200–2400. Error bars represent standard errors about each mean.

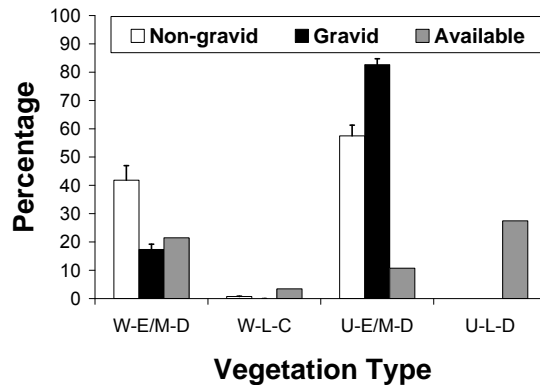


FIGURE 3. Percentage of location events for telemetered gravid and non-gravid females in each vegetation type at PCCI, and percentage availability of these vegetation types within the legal sections comprising the PCCI study area. W-E/M-D = early/mid-successional deciduous wetland, W-L-C = late successional coniferous wetland, U-E/M-D = early/mid-successional deciduous upland, U-L-D = late successional deciduous upland.

density), whereas gravid females must maintain high  $T_b$  despite energetic deficits to facilitate embryogenesis.

Gravid females maintained significantly higher  $T_b - T_a$  compared with non-gravids early (i.e., May) and late (i.e., July and August) in the season. This suggests thermoregulatory needs of gravid *S. c. catenatus* are greatest at cooler temperatures and during later developmental stages when embryonic metabolic requirements are increased (Schultz et al. 2008). Maintaining higher  $T_b$  by gravid females is especially critical, and may be problematic, in the Upper Great Lakes Region where summer temperatures range from 12.8°C to 28.8°C (Michigan State Climatologist’s Office. 2006. Available from <http://climate.geo.msu.edu/stations/3661> [Accessed 20 Nov 2006]).

Mean  $T_b$  of *S. c. catenatus* in 2005 was greater than 2004. Conversely,  $T_b - T_a$  was greater in 2004 than 2005. Inclement weather can limit attainment of optimal  $T_b$  (Peterson 1987), and we suspect lower temperatures in 2004 were driven by colder conditions during that year. Given that  $T_b - T_a$  was lower in 2005 (ostensibly meaning that females were thermoregulating less during the warmer year), mean  $T_b$  in 2005 (30.33°C) may more accurately reflect optimal  $T_b$ . This is consistent with the hypothesis that massasaugas invaded the area during the xerithermal and are having difficulty adjusting to more recent global cooling.

Gravid female *S. c. catenatus* at PCCI selected early/mid-successional deciduous upland vegetation. This was likely driven by higher mean soil temperatures in early/mid-successional deciduous uplands than in early/mid-successional wetlands (19.9°C and 17.4°C, respectively). Others have documented similar vegetation selection patterns, but have not described how

vegetation selection patterns may have been influenced by thermal requirements. Gravid *S. c. catenatus* in Pennsylvania used the driest and most open sites available, especially late in gestation (Reinart and Kodrich 1982), and gravid snakes in Ontario, Canada selected vegetation with less canopy closure than sites used by non-gravid females (Harvey and Weatherhead 2006). Many *S. c. catenatus* populations currently exist as isolated relicts, often exhibiting varied habits among populations (Syzmanski 1998; Johnson 2000). The ecological and spatial variability of *S. c. catenatus* has made large-scale conservation practices difficult to develop and implement (Syzmanski 1998). Consistent selection of early/mid-successional upland vegetation, in Michigan, Pennsylvania (Reinart and Kodrich 1982), and Ontario (Harvey and Weatherhead 2006) suggests this vegetation type may be desirable for gravid female *S. c. catenatus* rangewide.

*Sistrurus c. catenatus* at YSRA did not use early successional uplands, but were located exclusively in early/mid-successional shrub-scrub fen. This is similar to a population of *S. c. catenatus* in New York that preferred peatland to forested swamp (Johnson 2000). Late successional vegetation (72%) dominated YSRA and the fen where *S. c. catenatus* occurred was almost completely surrounded by upland deciduous forest. Thus, lack of use of early/mid-successional uplands at YSRA may reflect lack of connectivity between this vegetation type and the fen, as well as a reluctance of *S. c. catenatus* to traverse late-successional areas. It is important to note, however, that mean soil temperature and  $T_b$  of gravid female *S. c. catenatus* in 2005 were similar between PCCI and YSRA. This suggests that

early/mid-successional shrub-scrub fen was thermally equivalent to early/mid-successional upland vegetation.

Similarities in vegetation selection patterns among study locations including PCCI indicates that early/mid-successional uplands, when available, are desirable to gravid *S. c. catenatus* throughout much of their range. These habitat selection patterns combined with our thermal data support the hypothesis that thermal needs are a proximate factor driving vegetation selection in gravid female *S. c. catenatus*. Thus, we recommend that upland areas adjacent to wetlands supporting *S. c. catenatus* should be maintained, thereby providing ample basking opportunities. Specifically, the growth and expansion of Autumn Olive (*Elaeagnus umbellata*) throughout PCCI may pose future challenges for maintaining EMR habitat (K. Bissell, pers. comm.). Although not addressed in this study, spatial heterogeneity also likely plays an important role in vegetation selection of *S. c. catenatus* (Harvey and Weatherhead 2006). Retreat sites (e.g., bushes, holes, woody debris, rocks) presumably are necessary to avoid predation and to facilitate precise thermoregulation (e.g., to maintain close to ambient temperature on very warm days, or to raise  $T_b$  above ambient temperature on cool days). This study underscores the importance of accessible early/mid-successional upland areas adjacent to wetlands for the reproductive success of *S. c. catenatus*. This vegetation type apparently provides gravid females with favorable thermal conditions, which ultimately may enhance *S. c. catenatus* productivity.

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### LITERATURE CITED

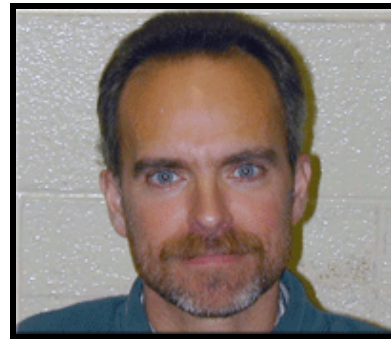
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