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ARTICLE

Identifying resilient Eastern Massasauga Rattlesnake (*Sistrurus catenatus*) peatland hummock hibernacula

A.G. Smolarz, P.A. Moore, C.E. Markle, and J.M. Waddington

Abstract: At the northern limit of the Eastern Massasauga Rattlesnake's (*Sistrurus catenatus* (Rafinesque, 1818)) range, individuals spend up to half the year overwintering. In hummock hibernacula found in peatlands, it is likely that subsurface temperature and water table position are contributing factors dictating habitat suitability. As a step towards assessing the vulnerability of hibernacula to anthropogenic changes, we combined subsurface temperature and water table dynamics to assess the likelihood that unflooded and unfrozen conditions were present in hummock hibernacula. Our results indicate that taller hummocks are more resilient to an advancing frost line and fluctuating water table by providing a larger area and duration of unfrozen and unflooded conditions, and a critical overwintering depth that is farther from the hummock surface. In two study sites along eastern Georgian Bay, an unflooded and unfrozen zone was present for over 90% of the overwintering period for hummocks taller than 25–27 cm. Our findings highlight the vulnerability of peatland hummocks to variability of winter weather where deep freezing and (or) water table rise may nonlinearly reduce resilience. This suggests that height is not the only component affecting the suitability of hummock hibernacula and that further research should examine the structure and spatial arrangement of hummocks within a peatland.

Key words: Eastern Massasauga Rattlesnake, Georgian Bay, Great Lakes, habitat, hibernacula, overwintering, *Sistrurus catenatus*.

Résumé : À la limite nord de l'aire de répartition des massasaugas (*Sistrurus catenatus* (Rafinesque, 1818)), les individus passent jusqu'à la moitié de l'année à hiverner. Dans des monticules servant d'hibernaculums dans des tourbières, il est probable que la température du sous-sol et la position de la nappe phréatique contribuent à moduler l'adéquation des habitats. Comme étape dans l'évaluation de la vulnérabilité des hibernaculums à des changements d'origine humaine, nous avons combiné la température du sous-sol et la dynamique de la nappe phréatique pour évaluer la probabilité de la présence de conditions non inondées et non gelées dans des hibernaculums en monticule. Nos résultats indiquent que les monticules plus hauts sont plus résilients en cas d'augmentations de la profondeur de gel et de fluctuations de la nappe phréatique, offrant des conditions non gelées et non inondées de plus longue durée et de plus grande superficie et une profondeur critique d'hivernage plus éloignée de la surface du monticule. Dans deux sites d'étude le long de la partie est de la baie Georgienne, une zone non inondée et non gelée était présente pendant plus de 90 % de la période de survie hiémale dans les monticules de plus de 25–27 cm de hauteur. Nos constatations soulignent la vulnérabilité des monticules de tourbières à la variabilité des conditions météorologiques hivernales là où le gel intense ou une hausse de la nappe phréatique pourrait réduire non linéairement la résilience. Cela indiquerait que la hauteur n'est pas le seul élément qui détermine si un hibernaculum en monticule est convenable, et que d'autres travaux devraient examiner la structure et l'organisation spatiale des monticules dans une tourbière. [Traduit par la Rédaction]

Mots-clés : massasauga, baie Georgienne, Grands Lacs, habitat, hibernaculum, survie hiémale, *Sistrurus catenatus*.

Introduction

At northern latitudes, where cold temperatures and the chance of snow can last up to half the year, reptiles must retreat underground and reduce their metabolic activity to survive the winter (Ultsch 1989). In addition to surviving harsh winter conditions, the majority of reptile species in Canada exist in ecosystems along the northern limit of their species' range where populations are less tolerant to environmental changes (García-Ramos and Kirkpatrick 1997). Such is the case for the Eastern Massasauga Rattlesnake (*Sistrurus catenatus* (Rafinesque, 1818); henceforth, Massasauga), a stout-bodied, venomous snake facing widespread declines in North America (Szymanski 1998; Pomara et al. 2014). Across the Massasauga's range, snakes use a variety of different habitats for overwintering including crayfish or small-mammal burrows (Seigel 1986), rooted wetland systems (Smith 2009), rock crevices (Wright 1941; Harvey and Weatherhead 2006), or peatland hummocks (Johnson 1995; Rouse and Willson 2002; Ministry of Natural Resources 2013).

Although Massasauga overwintering sites across their range are unique from a habitat perspective, the subterranean microenvironment must meet certain conditions and be resilient to external environmental changes to maximize winter survival of snakes. For example, snakes must overwinter below ground to seek shelter from cold air temperatures and avoid freezing (Gregory 1982). Therefore, snakes will overwinter below the frost line where temperatures are stable and cool to allow snakes to remain at a reduced metabolic state (Macartney et al. 1989; Ultsch 1989). The hibernacula must also provide protection from desiccation, a major threat to snakes during the winter (Costanzo 1986). Some species such as the Eastern Ribbonsnake (*Thamnophis sauritus* (Linnaeus, 1766)) and Massasauga have been observed to

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spend some of the winter submerged in water or with the head and external nares just above water presumably to access oxygen (Smith 2009; Todd et al. 2009). However, other species are less tolerant to flooded conditions. Gillingham and Carpenter (1978) observed snakes (i.e., Western Rat Snake, *Pantherophis obsoletus* (Say, 1823); Great Plains Rat Snake, *Pantherophis emoryi* (Baird and Girard, 1853); Pine Snake, *Pituophis melanoleucus* (Daudin, 1803); Copperhead, *Agkistrodon contortrix* (Linnaeus, 1766)) in constructed hibernacula and found higher mortality rates were primarily attributed to flooding of the hibernacula. Therefore, if a species is less tolerant to flooded conditions, then suitable hibernacula must balance both oxygen and moisture requirements to maximize successful overwintering.

Physiological adaptations such as the ability to tolerate anoxia would permit species to hibernate in or endure flooded conditions (Ultsch 1989; Storey 1996). Although anoxia tolerance has never been studied in Massasaugas, a mass mortality event of snakes along Georgian Bay, Lake Huron, in the winter of 2014–2015 is thought to have occurred either during a cold period before the first significant snowfall, which may have caused the snakes to freeze, or after spring snowmelt whereby the Massasaugas may have drowned in the hummocks (R. Black and M. Colley, personal communication, 2016). Moreover, reduced suitability of hibernacula in mined peatlands because of their vulnerability to flooding (Parks Canada Agency 2015) supports Massasauga's sensitivity to flooding events. Even in more southern parts of the Massasauga's range, snakes hibernated in sites where the water table was close to the surface, but safe from flooding (Smith 2009). Although Massasaugas are likely able to tolerate short-term inundation, long-term flooding and water level fluctuations may be detrimental (Shine and Mason 2004; Smith 2009). Therefore, the presence of an area above the water table and below the frost line would provide Massasaugas (*i*) protection from freezing, (*ii*) access to oxygen thereby minimizing exposure to anoxic conditions, and (*iii*) either access to the water table or a moist environment to prevent desiccation. We refer to the unfrozen and unflooded area as the zone of resilience; an area that provides access to oxygen while also buffering against an advancing frost line and a fluctuating water table to minimize the chance of Massasaugas drowning or freezing within the hibernacula.

Georgian Bay is one of four remaining locations supporting Massasaugas in Ontario, Canada, and occurs at the species' northern range limit (Rouse and Willson 2002; Parks Canada Agency 2015). Although the Georgian Bay population is thought to be large and stable (Parks Canada Agency 2015), subpopulations of Massasaugas in these areas continue to face threats such as persecution, habitat loss, and habitat fragmentation that have resulted in their designation as a threatened species (Ontario Government 2007; COSEWIC 2012). In particular, protection of peatlands is critical to long-term population persistence because individual Massasaugas demonstrate fidelity to peatlands for hibernation and suitable hibernacula are often limited (Harvey and Weatherhead 2006; Parks Canada Agency 2015; Rogers 2015). Unlike the majority of Massasauga hibernacula, the primary overwintering habitat for northern populations along Georgian Bay, Lake Huron, are peatland hummocks (Parks Canada Agency 2015). Peatlands typically feature a diverse microtopography consisting of *Sphagnum* L. moss species forming hummocks and hollows (Clymo 1973; Rydin 1993). Hummocks are raised mounds above the water table and hollows are the surrounding flat, low areas (Rydin 1986; Nungesser 2003). Hummocks provide critical hibernation habitat because of their unique ability to retain moisture. *Sphagnum* moss species that characterize hummocks avoid desiccation (Titus and Wagner 1984) and stay moist longer under dry conditions (Hayward and Clymo 1982; Strack and Price 2009) because of their ability to draw water upwards from a depressed water table (Titus and Wagner 1984). Thus, even when the water table is below the wetland surface, the unique dynamics of peatland hummocks could provide snakes with a moist hibernaculum, a vital characteristic of a suitable overwintering site (Costanzo 1986). In light of the ecohydrological properties of *Sphagnum*, peatland hummocks can provide a zone of resilience to buffer against frost penetration and a fluctuating water table, opportunities for aerobic respiration, and moisture to prevent desiccation if the water table is inaccessible.

The size and (or) height of the peatland hummock may also be important to ensure that snakes can adjust their position if faced with temperature or water table fluctuations (Sexton and Marion 1981; Macartney et al. 1989). Moreover, availability of multiple hummocks within a peatland may be important, as snakes have been shown to move overland within their overwintering sites to new holes before the first snowfall (Smith 2009). Microclimate within the hummock is critical for snakes to maintain an optimal body temperature; therefore, snow depth, duration of snow cover, and timing of snowfall may be important components of hibernaculum suitability because snow acts as an insulator, reducing heat loss in the winter and controlling the extent of frost penetration (Zhang 2005). A rapid mid-winter or spring snowpack melt can increase peatland water levels (Ketcheson et al. 2012) and potentially flood critical overwintering habitat for long periods of time. Therefore, snow accumulation and ablation (snow melt) processes at the surface, including the influence of forest canopies (e.g., Pomeroy and Schmidt 1993; Hedstrom and Pomeroy 1998), are important components when evaluating the suitability of hummock hibernacula.

To better understand peatland hummock hibernation sites, we characterized the thermal and water table dynamics in hummocks across two study areas along Georgian Bay, Lake Huron. We hypothesized that hummock height is an important physical parameter dictating hibernation site suitability. We predicted that taller hummocks would be more effective at buffering against an advancing frost line and a fluctuating water table compared with shorter hummocks, and thus, provide a larger zone of resilience. To test this hypothesis, we created the resilience index as a way to integrate subsurface temperature and water table dynamics with hummock height to determine (*i*) the size of the zone of resilience (i.e., area that is unfrozen and unflooded), (*ii*) the depth below the hummock surface that maximizes time spent in the zone of resilience (critical depth), and (*iii*) the hummock height that maximizes the presence of the resilience zone. We also hypothesized that hummocks with a higher canopy cover would have lower snow cover, therefore impacting the thermal buffering in hummocks and resulting in deeper frost penetration. Characterizing the zone of resilience in hummock hibernation sites will enable us to determine hibernacula that are sensitive to impacts and identify suitable hibernacula that require protection.

Materials and methods

Study area and site characterization

We monitored Massasauga hummock hibernacula within two study areas along the eastern shoreline of Georgian Bay. Our northernmost site, located on Magnetawan First Nations land (henceforth MAG) was an open, poor fen (sedge-dominated, acidic peatland) surrounded by trees along the wetland margin. In the MAG peatland, we monitored six individual hummock hibernacula. Located south of the MAG was a densely forested peatland near Pointe au Baril (henceforth PAB). At PAB, we monitored 10 individual hummock hibernacula. Both peatlands in our study were confirmed as active Massasauga hibernation sites by local biologists conducting field surveys; however, the individual hummocks used by hibernating snakes were not confirmed. Monitored hummocks were selected to represent the range of hummock heights available in the peatland. At each instrumented hummock, we characterized hummock microtopography using a Smart Leveler (Digital Leveling Systems, Smyrna, Tennessee, USA) to determine hummock height, which was referenced to the closest groundwater well (<10 m) located in a hollow.

Within both study areas, we measured wetland area, peat depth, mean tree height, mean tree diameter at breast height (DBH), canopy openness, and tree-stand density. We measured wetland area by walking the perimeter and using the area calculation tool on a Garmin eTrex 10 GPS (Garmin International, Olathe, Kansas, USA). We measured peat depth every 0.5–1.0 m along three margin-to-middle transects by inserting 1.8 m rebar into the peat until it struck bedrock or underlying sediment. If the depth of the peat was greater than 1.8 m, then we recorded the measurement as >1.8 m.

We conducted tree surveys to determine tree-stand density and measured tree circumference at breast height (converted to DBH) in one randomly placed 15 m by 15 m quadrat. The surveyed quadrat included a portion of both margin and interior. We measured tree heights using the Smart Measure application (Smart Tools co. version 1.6.6, M-D Building Products, Oklahoma City, Oklahoma, USA), which uses trigonometric relations to estimate tree height (±0.1 m accuracy from ground truthing).

Canopy openness was measured at each instrumented hummock by taking photographs using a Sunex 185° SuperFisheye 5.6 mm F/5.6 lens on a Canon EOS Rebel DSLR camera. The camera was pointed north and placed on a levelled surface. We processed photographs using the Gap Light Analyzer software (Cary Institute of Ecosystem Studies, Millbrook, New York, USA) to estimate canopy cover and openness (Frazer et al. 1999).

Thermal and hydrological data

We instrumented both study areas for the winters of 2015–2016 and 2016–2017 to collect air temperature, soil temperature, and water table depth data.

We recorded water table depth (m) every 10 min at both sites in a 1–2 m deep groundwater well using self-logging Levelogger Junior pressure transducers (Solinst, Georgetown, Ontario, Canada) and corrected for changes in atmospheric pressure using a Barologger Edge barometric logger (Solinst, Georgetown, Ontario, Canada) or a Levelogger Junior pressure transducer (Solinst, Georgetown, Ontario, Canada). We recorded mean air temperature (°C) at 30 min intervals using an HMP60 temperature–relative humidity probe (Campbell Scientific, Inc., Logan, Utah, USA). In both study areas, we mounted equipment in a radiation shield 1.3 m above the ground. All data were logged and stored using a Campbell Scientific CR1000 data logger (Campbell Scientific, Inc., Logan, Utah, USA).

We recorded soil temperature at each of the hummock sites (6 in MAG, 10 in PAB) using Campbell Scientific CS655 probes (probe length 12 cm; Campbell Scientific, Inc., Logan, Utah, USA) or T-type thermocouple wire (Omega Engineering, Norwalk, Connecticut, USA). Soil temperature was recorded at depths of 1, 5, 10, 15, 25, and 50 cm relative to the top of the hummock. We considered the temperature measurement at 1 cm to represent the surface, as exposure to sunlight and near-surface microclimate fluctuations at 0 cm (actual surface) would occur and cause biased results.

We estimated frost depth through interpolation of the 0 °C isotherm from the soil temperature measurements (Lindström et al. 2002). This method for determining the frost line identifies points in time when the temperature at each depth falls below zero, which may be interpreted as a frost index (Maidment 1993; Lindström et al. 2002). As the frost line advanced and negative temperatures were detected deeper in the profile, it was assumed that any point above that depth was also frozen. Therefore, this method does not account for periods when the frost line was present despite the surface being thawed and deeper portions of the hummock remaining frozen.

In October 2016, we inserted wooden metre sticks into each instrumented hummock to determine the depth of snow above the hummock surface. We measured snow depths eight times throughout the winter of 2016–2017 (25 November 2016, 13 December 2016, 21 December 2016, 6 January 2017, 19 January 2017, 16 February 2017, 25 February 2017, and 1 March 2017).

Table 1. General site characteristics for monitored peatlands located in Pointe au Baril (PAB) and Magnetawan First Nation (MAG), Georgian Bay.

	PAB	MAG
Area (m^2)	10 000*	2 323
Tree density (trees/m^2)	0.44	0.32
Mean (±SD) DBH† (cm)	34.4±19.2	23.7±14.5
Mean (±SD) tree height (m)	11.0±4.8	5.2±2.3
Mean (±SD) canopy openness‡ (%)	33±7.0	48±6.8
Mean (±SD) middle peat depth (cm)	<180	50±17.4
Mean (±SD) margin peat depth (cm)	31±30.6	17±11.3

*Estimated (Rogers 2015).
†Diameter at breast height.
‡Value for monitored hummocks.

Resilience index

The resilience index is a scaled measure of the proportion of time an unflooded and unfrozen area is present within a hummock. The larger the zone of resilience and the longer it is present, the greater the buffering capacity against a descending frost line and fluctuating water table. A score of 0 indicates that no zone of resilience existed during the overwintering period and that no area within the monitored portion of the hummock (surface to 80 cm) was unflooded and unfrozen. A score of 1 indicates that the zone of resilience encompassed the entire monitored portion of the hummock (surface to 80 cm) during the overwintering period, and thus, the entire area was unflooded and unfrozen. To create the resilience index, we used soil temperature and water table depth data to determine the percentage of time that each 5 cm depth interval, in each hummock, was flooded, frozen, flooded or frozen, or neither from 1 October to 31 May. The flooded or frozen zone was included to account for uncertainty when temperatures hovered near 0 °C and interaction with the water table could have resulted in either state. We used the period between 1 October and 31 May because it encompasses the time when snake ingress and egress would be occurring at the overwintering site (Harvey and Weatherhead 2006; Parks Canada Agency 2015). The *y* axis on the resilience index was set to 80 cm because the water table never dropped below this depth. We defined the critical depth as the depth that maximizes the probability of being unfrozen and unflooded during the overwintering season (i.e., point of intersection between the frost line and the water table line). Next, we used the trapezoidal numerical integration function in MATLAB version 9.2 (MathWorks, Inc., Natick, Massachusetts, USA) to calculate the "area" that the resilience zone occupied in the graph space and scaled the index between 0 and 1.

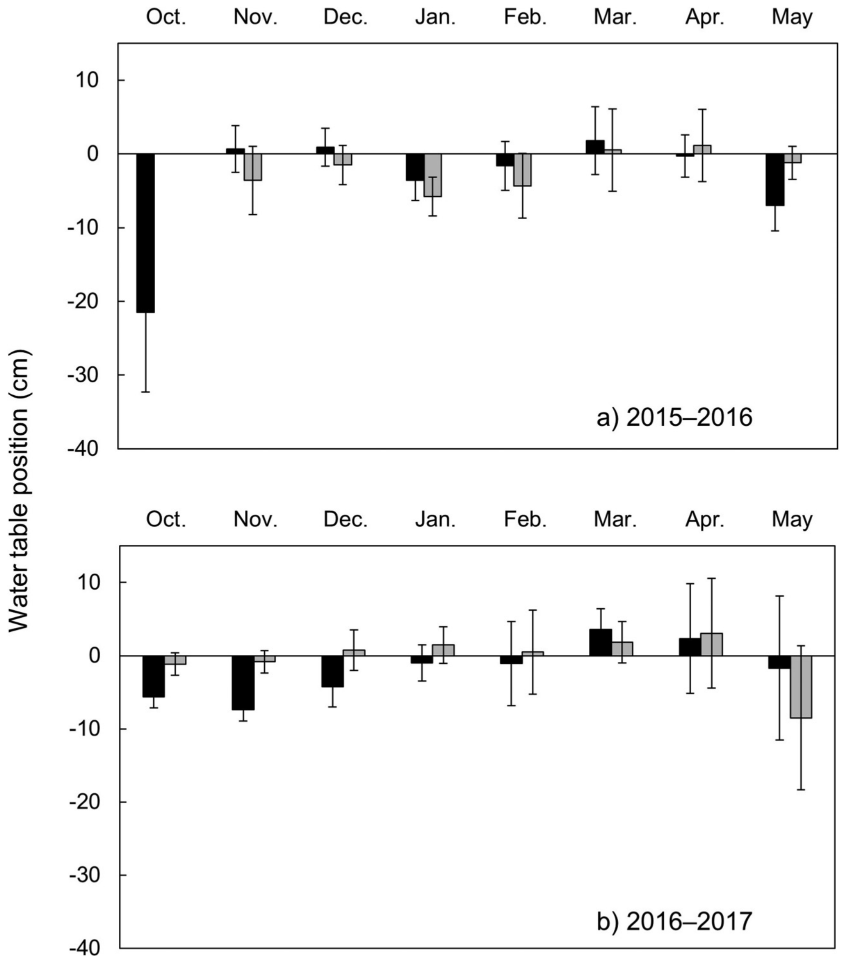
We used regression analyses to test the relationship between resilience index and hummock height, determine the depth at which the unfrozen and unflooded area is maximized, and the duration an unfrozen and unflooded area was present. All regressions were performed in JMP version 13 (SAS Institute Inc., Cary, North Carolina, USA) and significance accepted at $\alpha = 0.05$. Unless otherwise stated, mean values are reported with standard error in parentheses.

Results

Site characterizations

We instrumented hummocks within two peatlands in eastern Georgian Bay (Table 1). In total, we monitored 6 hummocks in MAG and 10 hummocks in PAB. Mean hummock height was 23 cm (±1.9 cm) in MAG and 27 cm (±1.4 cm) in PAB. Across sites, monitored hummock heights ranged from 13.2 to 32.3 cm, with a mean

Fig. 1. Monthly water table position (mean ± SD) relative to hollow surface for the (*a*) 2015–2016 overwintering period and (*b*) 2016–2017 overwintering period for peatlands studied in Pointe au Baril (grey bars) and Magnetawan (black bars).



height of 25 cm (±0.8 cm). PAB was a larger and deeper peatland compared with MAG, characterized by larger trees, higher tree density, and lower mean canopy openness above monitored hummocks (see Table 1).

Thermal and hydrological parameters

Water table generally increased throughout the winter, and in a few instances, rose above the hollow surface (Figs. 1*a*, 1*b*). The water table tended to be most variable later in the season (e.g., February–May; Figs. 1*a*, 1*b*). Mean snow depth during the overwintering period was shallower at MAG (20 ± 2.6 cm) than PAB (37 ± 2.4 cm). At the beginning and end of the overwintering period, when no consistent snow cover was present, hummock temperature patterns were more consistent with air temperatures (Supplementary Figs. S1*a*, S1*b*).[1] Once snow cover became persistent, hummock temperature stabilized (Supplementary Fig. S1*a*, S1*b*)[1] despite air temperature frequently dropping below –10 °C and daily temperatures fluctuating by over 15 °C (Supplementary Figs. S1*c*, S1*d*).[1]

Resilience index

For each of the 16 monitored hummocks, we calculated the percentage of time that each depth was flooded, frozen, flooded or frozen, or unflooded and unfrozen during the overwintering period to determine the resilience index score (Figs. 2*a*, 2*b*).

We found that the resilience index score increased as hummock height increased in PAB ($R^2 = 0.68$, $F_{[1,18]} = 37.7$, $p < 0.001$; Fig. 3) and MAG ($R^2 = 0.63$, $F_{[1,10]} = 16.7$, $p = 0.002$; Fig. 3); however, the resilience index score never exceeded 0.4. We also found that the depth which maximizes the amount of time spent in the unflooded and unfrozen area (critical depth) was farther below the hummock surface as height increased ($R^2 = 0.63$, $F_{[2,29]} = 24.6$, $p < 0.001$; Figs. 4, 5*a*). Across all hummock heights, this resulted in the critical depth occurring approximately 10 cm above the base of the hummock. Even at the critical depth, taller hummocks still tended to be unflooded and unfrozen for a greater percentage of the winter (Fig. 5*b*); however, this relationship was steeper in PAB hummocks ($R^2 = 0.66$, $F_{[1,18]} = 35.4$, $p < 0.001$; Fig. 6) compared with MAG hummocks ($R^2 = 0.26$, $F_{[1,10]} = 3.4$, $p = 0.09$; Fig. 6). At the critical depth, hummocks in MAG provided an unflooded and unfrozen area over 90% of the overwintering period (Fig. 6). In particular, hummocks taller than 25 cm provided a zone of resilience over 96% of the time. Generally, PAB hummocks taller than 27 cm provided a zone of resilience over 90% of the time (Fig. 6). Even at the critical depth in PAB hummocks, any hummocks shorter than 22 cm were unflooded and unfrozen only 77%–83% of the overwintering period.

We also observed a weak and positive trend that taller hummocks tended to be unflooded and unfrozen more often within

[1]Supplementary figures are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0334.

Fig. 2. Example of the delineation of flooded, frozen, flooded or frozen, and unflooded and unfrozen zones within a (*a*) short (20 cm height) and (*b*) tall (31 cm height) hummock during the winter of 2015–2016. The intersection point between the frost line and water table indicates the depth at which unflooded and unfrozen conditions are maximized.

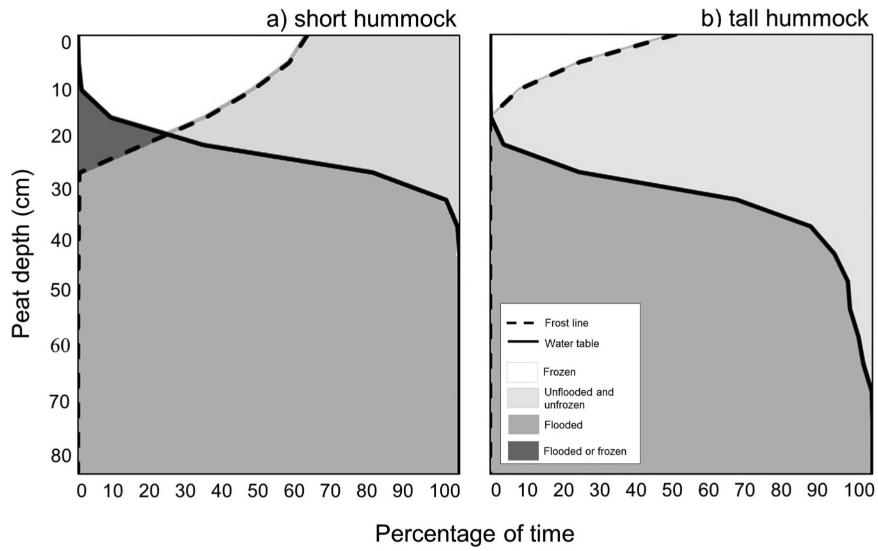
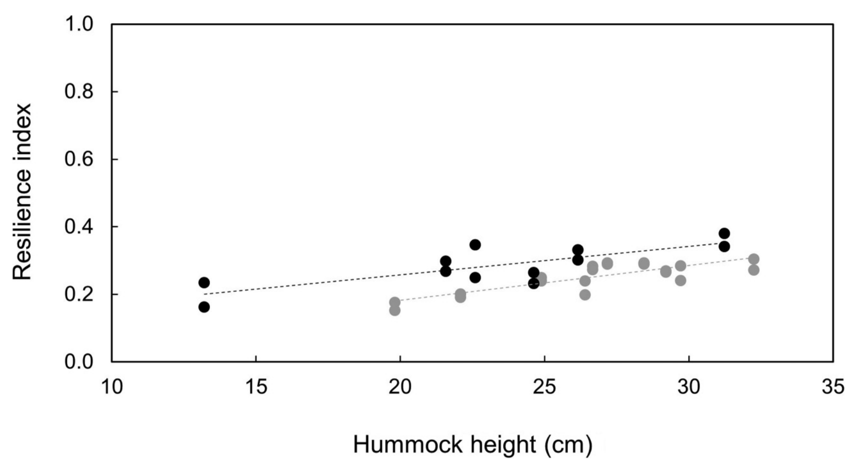


Fig. 3. Resilience index for the 16 hummocks monitored in Pointe au Baril (grey circles) and Magnetawan (black circles) during the 2015–2016 and 2016–2017 overwintering seasons.



10 cm above or below the critical depth (see Supplementary Figs. S2*a*, S2*b*).[1] For example, a tall hummock (height of 31 cm) was unflooded and unfrozen 100% of the overwintering period at the critical depth of 15 cm (Fig. 2*b*). Even at depths ranging from 5 to 25 cm, a zone of resilience occurred 80% of the overwintering season (Fig. 2*b*, Supplementary Figs. S2*a*, S2*b*[1]). In comparison, in a short hummock (height of 20 cm), unflooded and unfrozen conditions were maximized at a critical depth of 20 cm; however, even at this depth, a zone of resilience was only present 75% of the overwintering period (Fig. 2*a*). A change in depth by ±10 cm reduces the occurrence of a resilience zone to less than 50% of the time (Fig. 2*a*, Supplementary Figs. S2*a*, S2*b*[1]).

Discussion

For a species that spends almost half its life hibernating, the location and suitability of Massasauga overwintering habitat is critical to their survival. Our results suggest that taller hummocks buffer an advancing frost line and fluctuating water table by providing a larger zone of resilience, critical overwintering depth farther from the hummock surface, and higher probability of unflooded and unfrozen conditions during the overwintering period (Figs. 5*a*, 5*b*). Taken together, these findings support our hypothesis that hummock height is an important factor impacting the suitability of hibernacula. Although taller hummocks had a larger area that did not freeze or flood providing a greater availability of suitable overwintering habitat, the resilience index score never exceeded 0.4. This means that the area which is unflooded and unfrozen is limited. Selection of this area would provide protection from freezing, access to oxygen thereby minimizing exposure to anoxic conditions, and a moist microenvironment if access to the water table is limited. Even with a larger zone of resilience, the presence of unflooded and unfrozen conditions can still vary temporally. Thus, a snake should hibernate at the depth that maximizes the amount of time spent in the zone of resilience or, what we refer to as, the critical depth. We found that the critical depth was farther from the hummock surface as the height of the hummock increased. This resulted in the critical depth occurring 10 cm above the base of the hummock. Furthermore, even at the critical depth, taller hummocks still provided more opportunities for hibernation within an unflooded and unfrozen area. This was especially pronounced in the PAB hummocks. Although MAG hummock heights displayed a weak relationship with size of the unflooded and unfrozen area 10 cm above and below the critical depth, this indicates that a variety of

Fig. 4. The depth where unflooded and unfrozen conditions occur for the greatest amount of time (critical depth) for the 16 hummocks in Magnetawan (black circles) and Pointe au Baril (grey circles).

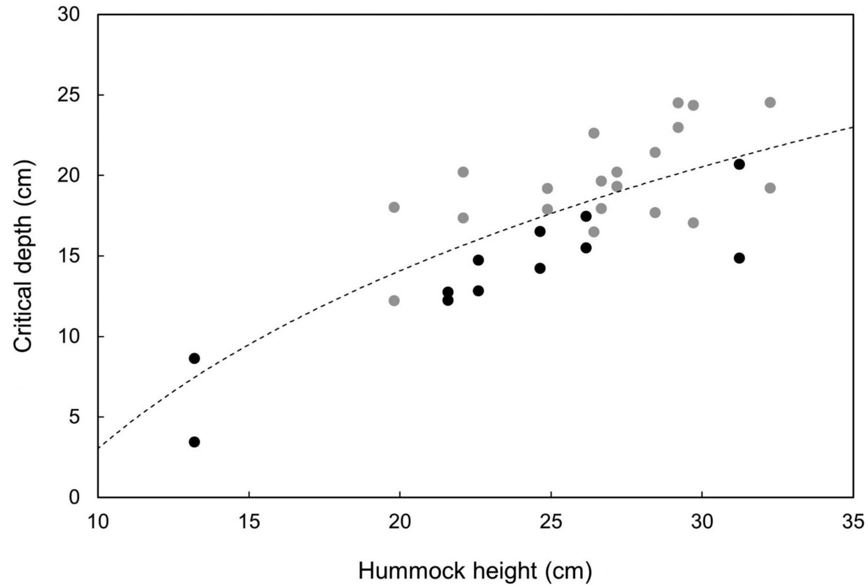
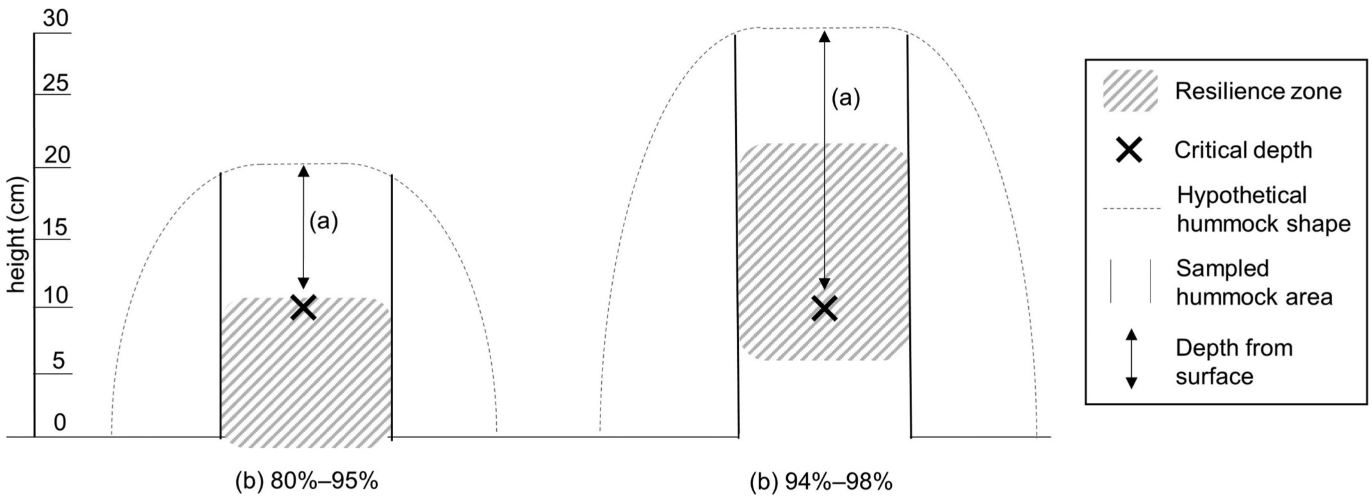


Fig. 5. The resilience zone (unflooded and unfrozen area) increases with hummock height, and therefore, the hummock has a larger area to buffer fluctuations in frost line and water table position. As hummock height increases, the depth that maximizes time spent in the resilience zone (×) is located farther from the surface (*a*) and the total duration of unfrozen and unflooded conditions also increases (*b*).

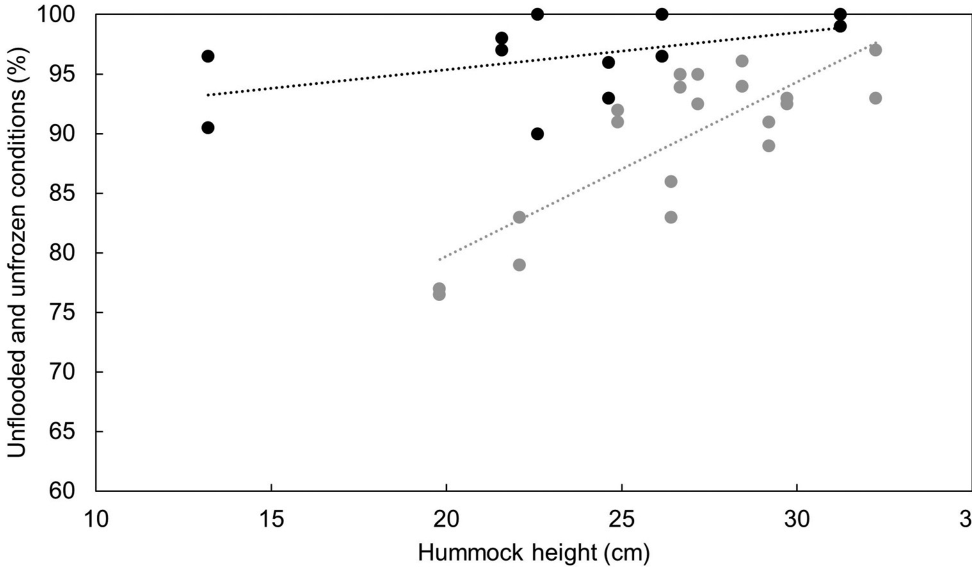


hummock heights provided relatively similar durations of unflooded and unfrozen conditions at critical depths. Therefore, in some peatlands, height is likely not the only factor contributing to the suitability of hummock hibernacula and other important factors may include the width, structure, and spatial arrangement of hummocks.

Our data demonstrate that depths where the duration of unflooded and unfrozen conditions are maximized is 20–25 cm below the surface in hummocks 30–35 cm tall. Moreover, after a certain point, the size of the hummock likely will not matter because the critical depth appears to reach a threshold in hummocks 25–30 cm tall. The location of the critical depth is also dependent on the ecohydrological feedbacks controlling hummock growth such as feedbacks between moss growth and (or) peat decomposition with peatland water table positions or water residence time (Waddington et al. 2015).

Tree density and canopy openness may provide some information on the suitability of various peatlands as hibernation sites. We hypothesized that hummocks with a higher canopy cover would lead to lower snow cover, and thus reduce the suitability of overwintering hummocks. This was not supported because PAB had a lower canopy openness (33% vs. 48%, respectively) and a slightly higher tree density compared with MAG (0.44 vs. 0.32 trees/m^2, respectively), but PAB had more snow cover (37 vs. 20 cm, respectively). Although MAG hummocks had less snow compared with PAB, hummocks of various heights within MAG provided a relatively stable resilience zone. In addition, we observed that hummocks at PAB tended to have snow present later into the spring. Snow remaining on the ground is likely due to shading from trees that prevents direct sun exposure for extended periods. Although the extended period of snow could delay snake emergence, it may help to protect the snakes during periods of fluctuating temperatures throughout the spring. We suspect that the discrete collection of snow depths does not accurately reflect the true snow cover conditions experienced throughout the winter. We suggest that future research continuously monitor snow depth to better characterize the importance of snow pack on hibernacula suitability. In particular, attention should be given to

Fig. 6. Percentage of time during the overwintering period that conditions were unfrozen and unflooded within hummocks at Pointe au Baril (grey circles) and Magnetawan (black circles). Conditions were calculated at the depth where unflooded and unfrozen conditions are maximized (critical depth).



the timing of the first substantial snowfall in relation to the first freeze, as well as durations of freeze and thaw events during spring emergence.

Mean monthly water table position in PAB and MAG demonstrate how close the water table can be to the peatland surface in the winter, and is consistent with research that Massasaugas select habitats where the water table remains relatively high and constant but is deep enough to prevent flooding (Smith 2009). Overwintering in taller hummocks provides snakes with a greater chance of protection from freezing and drowning. However, if climate change alters the timing or magnitude of flooding or anthropogenic disturbances alter peat properties, then these stressors can lead to changes in the mean water table position (Waddington et al. 2015). As a result of such changes, the already limited number of suitable hibernacula may no longer meet the needs of the Massasaugas. For instance, the timing of flooding and drought within peatland overwintering sites thus becomes increasingly important.

Intentional water table manipulations to raise or drop groundwater levels during the winter using levees or dikes has been suggested as a strategy to manage hibernacula (Johnson et al. 2000; Shine and Mason 2004). However, water table manipulations are not always practical and may be prohibitively expensive unless structures are already in place (Johnson et al. 2000). Even then, we strongly caution against the use of such structures because limited knowledge exists regarding the survivals rates of Massasaugas as a result of various water table manipulation strategies during hibernation. Therefore, the primary approach should be conserving the remaining peatland overwintering sites. In projects where the goal is to restore hibernacula, strategies should consider use of natural vegetation to minimize summer drought and winter flooding events (Pomara et al. 2014). Peatlands particularly could benefit from this approach, as the natural ground and moss cover contribute to a stable water table because of their ability to store and take up water (Waddington et al. 2015). Conservation strategies should therefore consider surrounding uplands, marginal vegetation, and the impact of trees and ground cover as part of the mitigation or remediation plan.

Our study provides insight into the features that make hummock hibernacula more resilient to the harsh Canadian winters. Our study revealed that taller peatland hummocks have a larger zone of resilience and higher resilience index score, and therefore a greater ability to buffer changes in water level and frost penetration. Furthermore, our results demonstrate that the zone of resilience is limited compared with areas that are flooded or frozen within a hummock. Improving our understanding of Massasauga hibernacula and the physical components that contribute to its suitability and resilience is a critical step towards identifying and protecting overwintering habitat, especially at the northern limit of the species' range where habitats are threatened by highway and cottage development (Rouse and Willson 2002).

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