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Original Research Article

Temporal variability of overwintering conditions for a species-at-risk snake: Implications for climate change and habitat management

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ARTICLE INFO

Article history:

Received 14 September 2019

Received in revised form 28 November 2019

Accepted 16 January 2020

Keywords:

Eastern Massasauga rattlesnake

Hibernacula

Peatland

Reptile

Sistrurus catenatus

Temperature

ABSTRACT

The suitability of overwintering habitat in response to temporal fluctuations in winter temperatures and water table position, and variability in timing and intensity of snowfall and rainfall is critical to informing management strategies for climate-sensitive species such as the Eastern Massasauga rattlesnake (*Sistrurus catenatus*). Important subterranean conditions contributing to the suitability of overwintering habitat for *S. catenatus* includes the availability of an unfloded space and temperatures above 0 °C which is conceptualized as the resilience zone. Here, we show that the timing and duration of resilience zone loss varies between years and among sites in response to variable weather conditions. Peatland habitat occupied by snakes lost the resilience zone fewer times and for shorter durations than unconfirmed habitat. In some cases occupied habitat continuously provided a resilience zone, suggesting that snakes may only be able to tolerate short periods of unsuitable conditions. As expected, larger precipitation events resulted in greater reduction of the resilience zone size. In particular, rain on snow events resulted in the greatest change in resilience zone size and could increase the risk of mortality events. With extreme weather-related events predicted to increase with climate change, long-term conservation of climate-sensitive species should focus on protecting habitats that are naturally resilient to changing and variable weather conditions and identifying vulnerable habitats that would benefit from additional research on adaptive management strategies.

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1. Introduction

Predicted increases in extreme weather-related events such as drought and flooding (Rahmstorf and Coumou, 2011; Donat et al., 2013) emphasize the importance of management strategies for species whose survival is tightly linked to water table dynamics (e.g., Matthews et al., 2013; Pomara et al., 2014). In particular, temporal variability of water table fluctuations can have a myriad of consequences for reptiles. For freshwater turtles, low water levels have resulted in altered movement patterns (Hall and Cuthbert, 2000; Anthonyamy et al., 2013), increased predation pressure (Stacy et al., 2014), increased susceptibility to disease transmission (Allender et al., 2011), and have been linked to mass mortalities (Hall and Cuthbert, 2000; Gasbarrini, 2017). In contrast, high water levels resulting in flooding have led to mass overwintering mortalities of

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snakes (Shine and Mason, 2004). Even annual winter mortality for some snake species has been reported as up to half of monitored individuals (Kingsbury et al., 2003; Harvey and Weatherhead, 2006). High rates of reptile mortality can have detrimental population-level impacts (e.g., Shine and Mason, 2004; Gasbarrini, 2017), and are of serious conservation concern since mass mortality events have drastically increased for reptiles beginning in the 1970s (Fey et al., 2015) and are associated with climatic events (Caughley, 1994).

In order to successfully develop and implement climate adaptation strategies, we must understand how species-at-risk habitat responds to variable weather events. The winter is a particularly vulnerable time for reptiles at northern latitudes, since they must retreat underground and seek shelter where they reduce their metabolic activity to survive the winter (Ultsch, 1989). Consequently, selection of suitable overwintering sites is a critical component of overwintering success and factors negatively affecting habitat suitability include water level fluctuations leading to freezing (Gregory, 1982; Shine and Mason, 2004), dehydration (Costanzo, 1989), or prolonged periods of flooding (Smith, 2009; OMNRF, 2016a). For species such as *Pantherophis obsoletus*, *Pantherophis emoryi*, *Pituophis melanoleucus*, and *Agkistrodon contortrix*, higher mortality rates in constructed hibernacula were attributed to flooding (Gillingham and Carpenter, 1978). The timing of flooding events can also result in early emergence from overwintering sites (Carpenter, 1953; Smith, 2009). Furthermore, high rates of winter mortality in natural sites suggest that suitable overwintering sites are limited in the landscape (e.g., Harvey and Weatherhead, 2006), which is supported by multiple snakes returning to the same general area (Johnson, 2000; Harvey and Weatherhead, 2006) or site (Shine and Mason, 2004) each year. Thus, suitability of overwintering sites into the future is a vital component to reptile population persistence especially since populations located near their current northern range limit may overwinter for almost half the year.

For a climate-sensitive species such as the Eastern Massasauga rattlesnake (*Sistrurus catenatus*; referred to as *massasauga*), taking immediate conservation action is vital for efficiently achieving improved outcomes and conservation goals (Naujokaitis-Lewis et al., 2018). The massasauga is considered a threatened or endangered species at the state/provincial or federal level across most of its range in the Great Lakes Region of Canada and the United States. To maximize the suitability of snake overwintering habitat, the subterranean microenvironment must provide shelter from freezing (Gregory, 1982), cool, stable temperatures to allow snakes to remain at a reduced metabolic state (Macartney et al., 1989; Ultsch, 1989), and protection from desiccation (Costanzo, 1989) without flooding for extended periods of time unless the species is able to tolerate anoxic conditions (Ultsch, 1989; Storey, 1996). Although massasauga's ability to tolerate anoxia and prolonged periods of flooding is relatively unknown, individuals have been observed submerged or partially submerged with the head and external nares above water presumably to access oxygen (Smith, 2009). Furthermore, massasaugas have been found to overwinter in sites that are safe from flooding (Smith, 2009; OMNRF, 2016a). While it is likely that massasaugas can tolerate short term inundation, evidence suggests that long term flooding and water level fluctuations may be detrimental (Shine and Mason, 2004; Smith, 2009; Yagi, K. pers comm, 2019). Therefore, the presence of a subterranean zone which provides massasaugas protection from temperatures below 0 °C and flooded conditions increases overwintering habitat suitability and is likely to be important for overwintering survival (Ultsch, 1989; Smith, 2009; COSEWIC, 2012; Yagi, K. pers comm, 2019).

One way to conceptualize suitable overwintering habitat is through the resilience zone which is defined as an unflooded space where temperatures are above 0 °C to minimize the risk of drowning or freezing (Smolarz et al., 2018). Changes in overwintering habitat suitability in response to temporal fluctuations in winter temperatures and water table position, and variability in timing and intensity of snowfall and rainfall is critical to informing management strategies for the at-risk massasauga especially in light of climate change. Therefore, our objective was to quantify the temporal fluctuations of peat temperature and water table position in peatland overwintering sites occupied by massasaugas and peatland habitat unconfirmed as overwintering habitat across two winters. We quantified the resilience zone as the space available that was simultaneously unflooded and above 0 °C during the overwintering season (Smolarz et al., 2018). If the resilience zone was lost, we determined the frequency, timing, and duration of these events between occupied and unconfirmed overwintering peatlands and between a relatively dry and wet winter season. We predicted that occupied overwintering habitat would provide a stable resilience zone. Second, we modeled how various water sources (rainfall, snowmelt, or rain on snow) and the size of input affected resilience zone response, predicting that larger precipitation events would have a greater effect on the resilience zone size. Understanding resilience zone dynamics in response to weather events will aid in the protection of peatland habitat and inform management strategies for the at-risk massasauga across its range.

2. Methods

2.1. Field data

Of the four geographically distinct regions currently supporting massasaugas in Ontario, Canada, the eastern Georgian Bay population occurs at the species' current northern range limit (Rouse and Willson, 2002; OMNRF, 2016a). Massasaugas in this population often rely on peatland hummocks for overwintering (OMNRF, 2016a), similar to massasaugas in other parts of their range (Johnson, 2000; Marshall et al., 2006; Yagi, K. pers comm, 2019). Peatlands are wetlands that accumulate deep organic matter (greater than 40 cm) such as bogs. In the Georgian Bay rock barren landscape, these peatlands experience hydrologic fill and spill dynamics which means outflow only occurs once the water table exceeds a certain level (Spence and Woo, 2003). The peatland surface is typically characterized by a range of *Sphagnum* dominated

microforms, including hummocks which are raised up to several decimeters above the water table, and hollows which are the adjacent low-lying areas (Clymo, 1973; Rydin, 1993; Nungesser, 2003). Massasaugas have been sighted within a 1 km² area of all three of our study peatlands along the shoreline of Georgian Bay; however, only two of the peatlands have been confirmed as active overwintering sites by local biologists conducting field surveys. Although no massasaugas were confirmed to overwinter in the third peatland during 2018/2019 springtime emergence surveys, we only refer to this site as unconfirmed since multiple survey years are recommended to determine snake absence (OMNRF, 2016b). We refer to our study sites relative to each other, with our most southern monitored peatland referred to as the unconfirmed southern site. Approximately 25 km north of our southern site is our occupied central site, and another 25 km north of that is our occupied northern site.

At the northern site (0.15 ha), six hummocks were monitored during the 2015 and 2016 overwintering seasons. A total of ten hummocks were monitored at our central site (1.00 ha) during the 2015 and 2016 overwintering seasons, and at the southern site (0.23 ha), two hummocks were monitored in 2016. Although individual hummocks selected by overwintering snakes were not able to be confirmed, we selected hummocks that represented the range of heights available in the peatland. Hummock heights were measured using a Smart Leveler (Digital Leveling Systems, Smyrna, TN, USA) and referenced to the nearest groundwater well (<10 m). Heights of monitored hummocks ranged from 13–31 cm in the northern peatland, 19–32 cm in the central peatland, and 17–22 cm in the southern peatland and were selected to provide an assessment of the suitability of available hummocks in each peatland. We operationally defined the 2015 overwintering season from 1 October 2015 until 31 May 2016 and the 2016 overwintering season from 1 October 2016 until 31 May 2017. 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; OMNRF, 2016a). At each of the three peatlands, water table depth was recorded every 10 min in a groundwater well using self-logging Levelogger Junior pressure transducers (Solinst, Georgetown, Ontario, Canada) and corrected for changes in atmospheric pressure using a barometric logger (Barologger Edge, Solinst, Georgetown, Ontario, Canada). Peat temperature was recorded every 30 min at 1 cm, 5 cm, 10 cm, 15 cm, 25 cm, and 50 cm below the surface of the hummock. The only exception was three hummocks at the northern site with temperature data at 1 cm, 10 cm, and 50 cm, and hummocks at the southern site which did not have temperature data at 10 cm. All peat temperature data were measured using CS655 probes (length 12 cm, Campbell Scientific, Inc., Logan, Utah, USA) or T-type thermocouple wire (Omega Engineering, Norwalk, Connecticut, USA). Mean air temperature was recorded every 30 min using an HMP60 temperature-relative humidity probe (Campbell Scientific, Inc., Logan, Utah, USA), mounted 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). Lastly, we used daily total precipitation and daily depth of snow on the ground from the nearest Environment Canada weather station (<20 km from southern study site).

2.2. Change in resilience zone size

We quantified resilience zone size as the distance (cm) between the 0 °C isotherm and position of the water table (Smolarz et al., 2018). We used linear interpolation to estimate the depth of the 0 °C isotherm from peat temperature profiles and then calculated resilience zone size by subtracting the 0 °C depth from the water table depth every 30 min during the overwintering season.

The change in resilience zone size was analyzed separately for three types of hydrological events, and broadly characterized as a (i) rainfall event, (ii) snowmelt event, and (iii) rain on snow event causing melting. The first event type was defined by rain ≥ 1 mm and snowmelt with a water equivalent <1 mm. The second event type was defined by snowmelt with a water equivalent ≥ 1 mm and rain <1 mm. The third event type was defined by rain on snow with rain ≥ 1 mm and snowmelt with a water equivalent ≥ 1 mm. The start of a weather event was defined as a day with water input ≥ 1 mm after a minimum of a 1-day dry period and ended when daily water input was <1 mm or there was no snow on the ground (for snowmelt and rain on snow events only). Similar to Ali et al. (2015), we used total precipitation and air temperature data to separate water inputs into rainfall and snowmelt. Precipitation was assumed to be all rainfall when air temperature was above 0 °C (Juston et al., 2009; Ali et al., 2015). Precipitation was assumed to be all snowfall when air temperature was below 0 °C (Juston et al., 2009; Ali et al., 2015). We report snowfall depth in cm by assuming a 10:1 ratio of initial snowfall depth to snow water equivalent. We modeled snowmelt events using an hourly degree day model and assumed snowpack to melt with a degree-day factor (melt coefficient) of 4 mm/°C/day (Juston et al., 2009).

In R 3.5.1, we calculated the number of times the resilience zone was lost (when 0 °C isotherm and water table intersect), and the duration and timing of each loss. In JMP 14 (SAS Institute Inc., Cary, NC, USA), we used a Kruskal-Wallis test to compare input sizes of rainfall, snowmelt, and rain on snow events. Between overwintering seasons (2015 vs. 2016), we compared the number of times the resilience zone was lost, total time with no resilience zone, and duration of individual events of resilience zone loss using a Wilcoxon signed-rank test. Next, in R 3.5.1, we generated a linear mixed-effects model using resilience zone size (cm) as the response variable, the hydrological event type (rainfall, snowmelt, or rain on snow), total water input during the event (mm), and initial resilience zone size (cm) as fixed effects, and individual hummock nested within site as random effects. We assumed a gaussian distribution and checked the normal distribution of plotted residuals to confirm goodness of fit. Generalized variance inflation factors for all fixed effects were around one, therefore no parameters were excluded based on multi-collinearity.

3. Results

Resilience zone size fluctuated continuously throughout the overwintering season (Fig. 1) but appears to be less variable at occupied sites (Fig. 1a and b) compared to unconfirmed sites (Fig. 1c). The resilience zone was lost an average of 2–79 times per hummock during the two study winters, with some hummocks maintaining a resilience zone throughout the entire winter and other hummocks being flooded or below 0 °C throughout the entire profile over 150 times (Table 1). Specifically, 6 of the 16 hummocks in 2015 and 3 of the 18 hummocks in 2016 provided a continuous zone of unflooded conditions and peat temperatures above 0 °C (from surface to 50 cm below surface), and all of these hummocks occurred in peatlands confirmed to be actively used by massasaugas. Of the two hummocks in the unconfirmed peatland, both had frequent losses of the resilience zone. Although some hummocks at occupied overwintering sites did lose their resilience zone, it was only lost for an average of 41 min to 4 h 48 min per event. On the other hand, at the peatland with no confirmed overwintering snakes, overwintering sites were flooded, and peat temperature dropped below 0 °C for an average of over 6 days per event (Table 1). Although only two hummocks were monitored at the unconfirmed site, the range of hummock heights are comparable across

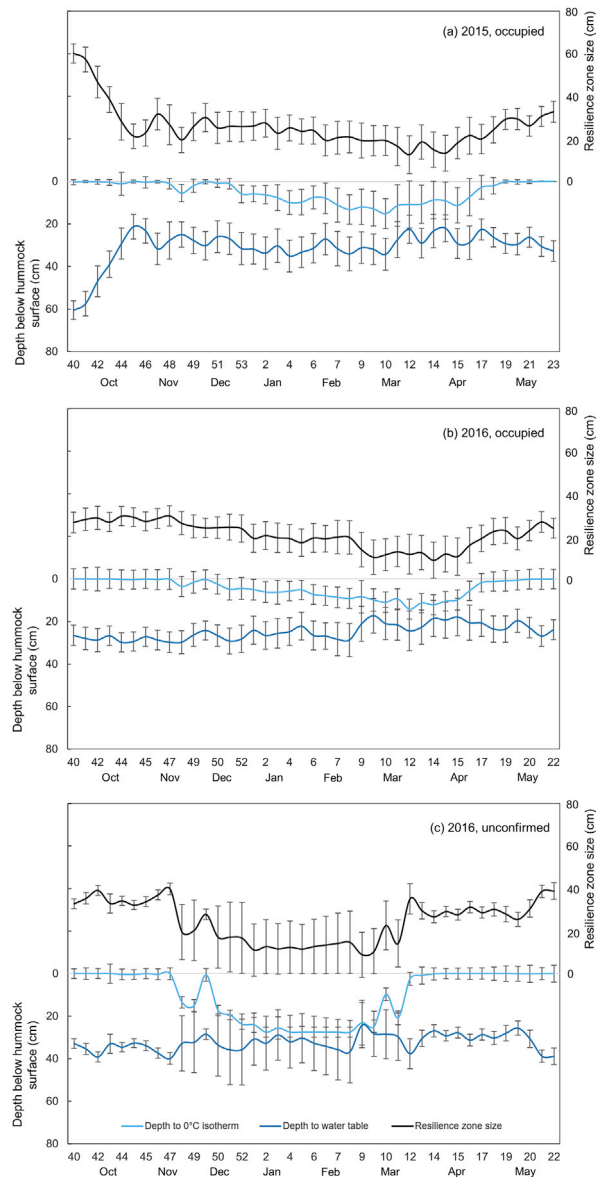


Fig. 1. Weekly mean depth \pm SD (cm) to 0 °C isotherm (light blue line) and water table (dark blue line) below the hummock surface and weekly mean size \pm SD (cm) of the resilience zone (black line) for all monitored hummocks in occupied overwintering peatland habitat in 2015 (a) and 2016 (b), and unconfirmed overwintering peatland habitat in 2016 (c). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

Table 1

Number of events and duration of resilience zone loss per hummock in occupied North (n = 6), occupied Central (n = 10), and unconfirmed South (n = 2) peatlands during the 2015 and 2016 overwintering seasons.

Site	Overwintering season	Mean total time resilience zone lost (\pm SE)	Mean number of events resilience zone lost (range)	Mean duration resilience zone lost per event (\pm SE)
Occupied North	2015	00 d, 03 h, 26 m (\pm 00:03:26)	2 (0–5)	0 h, 41 m (\pm 00:41)
	2016	00 d, 20 h, 49 m (\pm 00:12:51)	6 (0–18)	1 h, 37 m (\pm 00:50)
Occupied Central	2015	04 d, 18 h, 15 m (\pm 01:22:20)	32 (0–73)	2 h, 37 m (\pm 00:39)
	2016	17 d, 09 h, 19 m (\pm 03:18:59)	79 (31–154)	4 h, 48 m (\pm 00:34)
Unconfirmed South	2016	44 d, 22 h, 29 m (\pm 44:07:35)	4 (1–7)	6 d, 16 h, 27 m (\pm 6:01:33)

sites and yet we still observed at least a 33-fold increase in the mean duration of resilience zone loss per event (Table 1). In some instances, resilience zone size can contract and expand over a short timeframe (e.g., several days; Fig. 1) as a result of relatively rapid fluctuations in soil temperature (Fig. 2a) and water table position (Fig. 2b) where the loss and subsequent recovery of the resilience zone can occur over a matter of days.

The timing of resilience zone loss varied between years and among sites. In 2015, over 80% of the events and duration of flooded/below 0 °C peat temperatures occurred in March and April at the occupied central site when mean air temperatures were above 0 °C (Fig. 3a and b). Although the majority of individual events occurred in October at the occupied northern site (Fig. 3b), the greatest length of time without a resilience zone also occurred in March and April (Fig. 3a). In 2016, almost half of the events occurred in April for occupied sites when mean air temperature was over 5 °C (Fig. 3d), although the resilience zone was lost for the longest period of time in November and March (Fig. 3c; North vs. Central, respectively). In comparison, 50% of events occurred in December at the unconfirmed southern site when mean air temperature was below 0 °C (Fig. 3d) and were long lasting (Fig. 3c).

On average, the resilience zone was lost for longer during the 2016 winter (3.6 h) compared to the 2015 winter (1.6 h; Wilcoxon signed rank, $S = 50$, $p = 0.0034$). Similarly, the resilience zone was lost more often, on average, in 2016 (51 times) compared to 2015 (19 times; Wilcoxon signed rank, $S = 61$, $p = 0.0005$) and for a greater average total amount of time (11 d 5 h (2016) vs (2 d 17 h (2015); Wilcoxon signed rank, $S = 61$, $p = 0.0005$). The difference in resilience zone dynamics between the two overwintering seasons correspond with the difference in weather conditions (see Fig. 3 and Fig. 4). The 2016 season was characterized by cold average monthly temperatures from December until March (-4.0 °C), with warm average temperatures in the fall (October and November) and spring (April and May; Fig. 3). Most of the snowfall in the 2016 season occurred from December until February (172 cm) with small amounts occurring in November (7.1 cm) and March (15.7 cm) and no snowfall in April (Fig. 4b). This combination of snowfall and air temperatures resulted in additional snowmelt and rain on snow events, totaling an additional 200 mm of water input (70 mm of snowmelt, 130 mm of rain; Fig. 4b) compared to the 2015 season (Fig. 4a). Furthermore, compared to the long-term October to May average precipitation of 572 mm (1981–2010; determined from the nearest weather station), 2016 had above average total precipitation (623 mm) and 2015 had below average precipitation (508 mm) during the overwintering season. In comparison, the 2015 season had almost 40 cm of additional

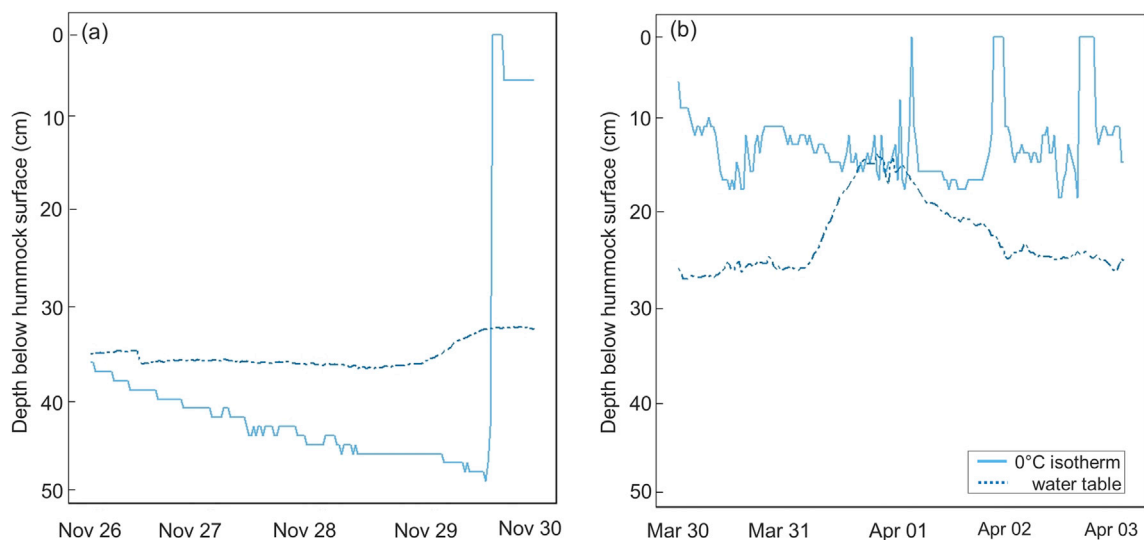


Fig. 2. Examples of rapid changes in the depth of the 0 °C isotherm (solid line) and position of the water table (dashed line) resulting in loss/recovery of the resilience zone for a few days due to temperature changes (a) or less than a day due to changes in water table position (b).

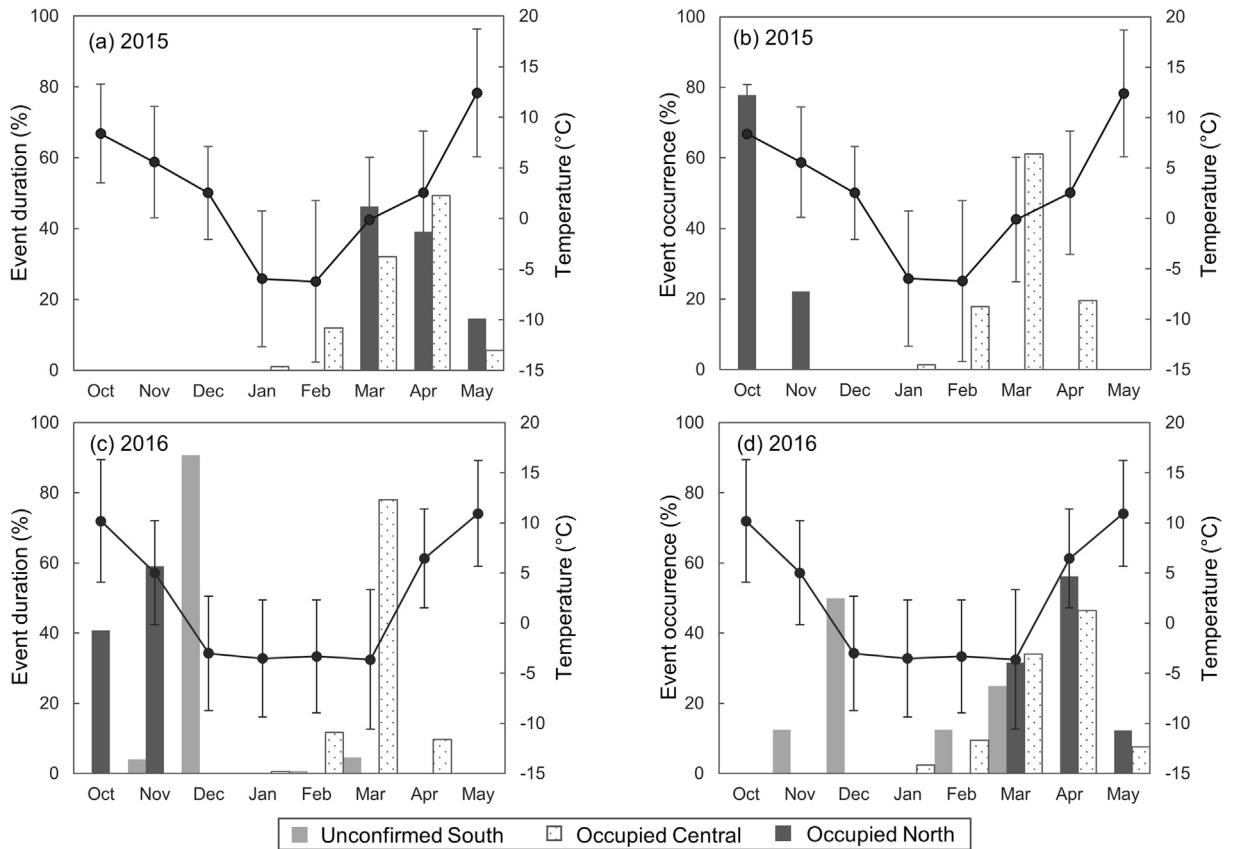


Fig. 3. Average monthly air temperature \pm SD ($^{\circ}$ C) during the 2015 (October 2015–May 2016) and 2016 (October 2016–May 2017) overwintering seasons (solid line). Event duration is the percentage of time the resilience zone was lost each month in 2015 (a) and 2016 (c) for the three surveyed peatlands (unconfirmed south (light grey bars), occupied central (stippled bars), occupied north (dark grey bars)). Event occurrence is the percentage of individual events that occurred each month during 2015 (b) and 2016 (d) for the three surveyed peatlands respectively.

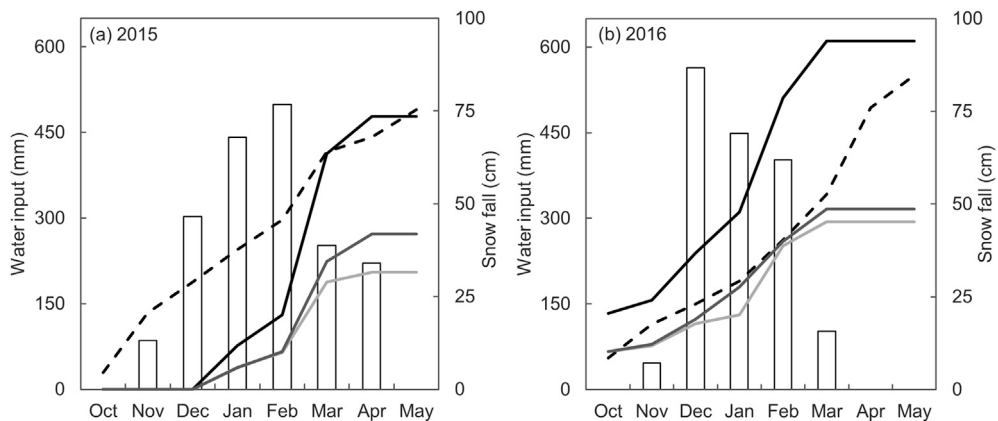


Fig. 4. Estimated monthly snowfall (cm; hollow bars) and cumulative monthly water input (mm) from rain on snow (light grey line), snowmelt (dark grey line), rain on snow and snowmelt events combined (black line), and rainfall (dashed line) for the 2015 (a) and 2016 (b) overwintering seasons.

snowfall compared to 2016, with an estimated monthly sum of 39–77 cm falling from December until April (Fig. 4). In the fall and early winter of 2015, average monthly air temperatures were above 0° C, dropping to -6° C for January and February. Although the mean air temperature was 3° C for April, temperature frequently dropped below 0° C unlike April in the 2016 season where air temperature was consistently above 0° C (Fig. 3). Overall, periods of wetter and warmer conditions in the 2016 overwintering season is reflected in a shallower water table depth and depth to the 0° C isotherm (e.g., Fig. S1).

Table 2

Results from the linear mixed effects model predicting the relationship between hydrological event type (rainfall, snowmelt, or rain on snow), total water input during the event (mm), and initial resilience zone size (cm) on the change in resilience zone size (cm).

Fixed effects	Estimate (\pm SE)	T value	P value
Input size	-0.095 (0.008)	-12.177	<0.0001
Type: snowmelt	-2.277 (0.371)	-6.124	<0.0001
Type: rain on snow	-1.586 (0.415)	-3.823	0.0001
Initial zone size	-0.109 (0.020)	-5.438	<0.0001
(Intercept)	-1.928 (2.221)	-0.868	0.466

Resilience zone size decreased during larger precipitation events, regardless of whether the input was from snowmelt, rain, or rain on snow (Table 2; Fig. S2). Although rainfall was the greatest source of water input in 2015 and the combination of snowmelt and rain on snow was the greatest source in 2016 (Fig. 4), discrete rain on snow events ($14.2 \text{ mm/day} \pm 2.0$) were a significantly larger source of water input than rainfall ($8.1 \text{ mm/day} \pm 1.1$) and snowmelt ($10.7 \text{ mm/day} \pm 1.7$; Kruskal-Wallis, $\chi^2 = 6.57$, $p = 0.04$) across both overwintering seasons. Furthermore, resilience zone size was reduced when the hummock had a larger initial resilience zone prior to the water input event (Table 2; Fig. S2).

4. Discussion

We found that resilience zone dynamics differed among and within peatlands, highlighting the importance of overwintering site selection at both the peatland and hummock scale by overwintering Eastern Massasauga rattlesnakes. As expected, occupied overwintering habitat provided a stable resilience zone (Fig. 1). At occupied peatlands, almost 40% of hummocks in 2015 (drier winter) and 17% in 2016 (wetter winter) provided a continuous zone of unflooded conditions and peat temperatures above 0°C from 1 October until 31 May. Although some hummocks at occupied overwintering sites did lose their resilience zone, it was only lost for an average of less than 5 h, suggesting that snakes can tolerate short periods of flooding and/or temperatures below 0°C . For example, massasaugas and the eastern ribbonsnake (*Thamnophis sauritus*) have been observed to spend some of the winter submerged or partially submerged with the head and external nares above water presumably to access oxygen (Smith, 2009; Todd et al., 2009). Although the duration of flooding conditions tolerated by massasaugas is unknown, massasaugas have been found to overwinter in sites that are safe from flooding (Smith, 2009; OMNRF, 2016a). If overwintering sites do flood, snakes may emerge early (Carpenter, 1953; Smith, 2009) and may be required to relocate to another overwintering site to access more suitable conditions. On the other hand, even though only two hummocks were monitored at the unconfirmed site, the hummocks were flooded, and/or peat temperature dropped below 0°C for an average of over 6 days each event. The marked difference in total time without a resilience zone between the unconfirmed and occupied sites occurred even though hummock height range was comparable. The variability and differences in timing and duration of resilience zone loss at the peatland and hummock scale suggests that additional factors beyond hummock height control the fine-scale temporal fluctuations in resilience zone size and habitat suitability and warrants further investigation.

Although snowpack is important for insulating peat temperature regardless of variable air temperatures (Zhang, 2005), the timing of air temperatures below 0°C is still a critical component of overwintering habitat suitability. For instance, at the occupied central site in the wetter season (2016), the resilience zone was lost in March when air temperature was still frequently dropping below 0°C and on other days when warm, rainy conditions quickly melted the snowpack. This combination of events can significantly reduce habitat suitability and even put snakes at risk of mortality if flooded conditions do not subside quickly since snakes may either drown or leave the hummock and risk exposure to freezing temperatures in subsequent cold snaps. That said, the loss of the resilience zone at the occupied central site in March was limited in duration (<3 h). On the other hand, the occupied northern site had the most resilient hummocks, even during the 2016 season, since the resilience zone was lost in months with mean air temperatures were above 0°C . In 2015, the northern site also had the highest proportion of hummocks that provided a zone of resilience continuously for the entire winter even though hummock heights were comparable to other monitored peatlands. Further research to determine site- and hummock-specific differences between the central and northern site would shed light on properties influencing habitat suitability and conveying this additional resilience to changing weather conditions.

While our study focused on peatland overwintering sites (Johnson, 2000; Rouse and Willson, 2002; OMNRF, 2013), our conceptualized resilience zone could serve as a useful metric supporting the assessment of habitat suitability for massasaugas which overwinter in other habitats such as burrows (Seigel and Pilgrim, 2002; Harvey and Weatherhead, 2006) and rock crevices (Harvey and Weatherhead, 2006) throughout their North American range. At any overwintering site, massasaugas select subterranean microhabitats that minimize the risk of freezing (Gregory, 1982) and where temperatures are fairly stable and permit a reduced metabolic state (Macartney et al., 1989; Ultsch, 1989). In addition, snakes must have access to water or moisture to prevent desiccation (Costanzo, 1989), but sites that minimize the risk of extended periods of flooding likely increase overwintering habitat suitability (Smith, 2009; Yagi, K., pers comm, 2019). Therefore, monitoring temperature and water level in any overwintering site across the massasauga's range can help monitor change in the resilience zone and thus provide an assessment of habitat suitability. Furthermore, continuous monitoring of water level and peat temperatures is

critical to provide an accurate assessment of overwintering conditions (e.g., Figs. 1 and 2). As we demonstrated, it is only with high temporal resolution data that we can identify times when the resilience zone is lost, more accurately determine what leads to the loss of the resilience zone, and how we can best manage the impact of changing conditions.

Determining when overwintering sites are most vulnerable to loss of the resilience zone will allow targeted conservation actions to improve our ability to adaptively manage at-risk massasauga populations immediately and in the long term. Although snowpack is important for insulating peat temperatures during cold winter air temperatures (Zhang, 2005), it can put overwintering sites at risk during warm, rainy days since rain and snowpack melt increases peatland water levels (Ketcheson et al., 2012). Although resilience zone size decreases during larger precipitation events, our results indicate that rain on snow events provided the largest source of water and could increase the risk of flooding. In line with this, our results also indicated that the resilience zone is more responsive to water input when the initial resilience zone size is larger. This is likely because if there is a small space that is unflooded/above 0 °C (i.e., small initial resilience zone) and it rains, it would not require much input to lose the resilience zone and result in runoff. In contrast, if there is a large space that is unflooded/above 0 °C (i.e., large initial resilience zone), the resilience zone would be able to decrease more without complete loss. Identifying this feedback is critical for management in a landscape with fill and spill dynamics because it highlights the importance of effective outflow. When there is a small initial resilience zone size, it is important that any additional water inputs will generate runoff. If the outflow is blocked, the water level can continue to rise effectively eliminating the resilience zone.

We advocate for a two-fold approach to optimize conservation of snake overwintering habitat in light of our findings and a changing climate; protection and enhancement or restoration. First and foremost, peatlands that are naturally resilient to flooding should receive the highest level of protection. Prioritizing the protection of naturally resilient systems provides immediate benefits to species at risk already occupying the habitat and is cost-effective (e.g., Dodds et al., 2008; Benayas et al., 2009; Possingham et al., 2015). A large-scale assessment of resilience zone dynamics across a variety of peatlands in space and time will allow such prioritization. Second, results from the large-scale assessment will likely identify peatland habitat that are vulnerable or already impacted by changing conditions but are currently occupied by overwintering snakes. Therefore, vulnerable occupied habitat would benefit from research into specific enhancement or restoration strategies to improve peatland and/or hummock resilience. Although hummock height provides resilience to individual hummocks (Smolarz et al., 2018), height is not the only factor because hummocks in occupied peatlands with heights ranging from 19 cm to 32 cm experienced loss of the resilience zone. By enhancing the resilience at the peatland-scale, occupied sites would be able to better respond and recover from rain on snow events. Determining that rain on snow events provide the greatest risk and identifying the importance of a functioning outflow is of critical conservation concern since the number of warm winter days where air temperature is above 0 °C could increase by up to 35 days in northern parts of the Great Lakes Basin (Zhang et al., 2018) and could result in more precipitation falling as rain, additional rain on snow events, or reduced snowpack. As an immediate action, conservation practitioners could monitor weather conditions for warm, rainy days with existing snowpack since these conditions have the potential to flood hibernacula. Collection of detailed elevation data would permit delineation of the peatland boundary and peatlands with single, narrow outflows like those with hydrologic fill and spill dynamics could be targeted for monitoring or candidates for restoration. The integration of protection, research, enhancement, and restoration is crucial for long-term management and conservation of species at risk and their habitats (Possingham et al., 2015).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was funded by a Seed Research Grant from the McMaster Centre for Climate Change. We thank Alanna Smolarz, Craig Allison, and Alex Furukawa for assistance in the field, and are grateful to Cory Kozmik, Ron Black, and Mike Colley for their support and assistance.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e00923>.

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