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Thermal Characteristics of Overwintering Habitats for the Blanding's Turtle (*Emydoidea blandingii*) Across Three Study Areas in Ontario, Canada

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***Abstract*.—Habitat restoration is a necessary strategy to protect populations of Blanding's Turtles (*Emydoidea blandingii*) living in settled areas. Relatively little is known about thermal tolerances and requirements of this species *in situ* during the overwintering period, except that these turtles must find water bodies that do not freeze completely and that are sufficiently cool to allow them to stay dormant throughout the winter. We used water temperature data associated with Blanding's Turtle populations in a northern, central, and southern study area within Ontario, Canada to determine thermal characteristics of occupied overwintering habitats. From fall through spring from 2012 to 2014, we measured water temperature of 20 potential overwintering habitats within the three study areas. We also radio tracked 48 adult turtles to determine which habitats they occupied during winter. Water temperatures of all occupied habitats ranged from 0.44° C to 3.68° C, with a mean of 1.77° C (± 0.03° C), and showed slow steady declines throughout the overwintering period. Regardless of location, average water temperatures at all confirmed overwintering habitats remained above the freezing point of turtle body fluids (-0.6° C). Average water temperature at five of the six confirmed overwintering habitats never dropped below 0° C, but dropped to -0.33° C for eight days at the sixth overwintering habitat. Determining thermal parameters of overwintering sites can provide knowledge useful for habitat restoration and creation to ensure habitats provide suitable overwintering conditions in the face of global climate change.**

Key Words.—Great Lakes; imperiled species; reptile, water temperature, wetland habitat

Introduction

The Blanding's Turtle (*Emydoidea blandingii*) is a northern species of freshwater turtle with populations concentrated around the Great Lakes, and isolated populations in New York, Massachusetts, New Hampshire, Maine, Pennsylvania, USA, and Nova Scotia, Canada (Congdon et al. 2008). Almost 20% of the Blanding's Turtles' range is located in Ontario, Canada, where the species is designated as Threatened (Ontario Government. 2007. Endangered Species Act. Available from http://www.ontario.ca/laws/statute/07e06 [Accessed 27 May 2016]). Throughout their range, adult Blanding's Turtles have been known to overwinter in a variety of aquatic habitat types including marshes (Kofron and Schreiber 1985; Rowe and Moll 1991; Joyal et al. 2001; Edge et al. 2009), swamps (Seburn 2010), bogs (Herman et al. 2003; Edge et al. 2009; Newton and Herman 2009), fens (Edge et al. 2009; Newton and Herman 2009), vernal pools (Joyal et al. 2001; Seburn 2010), streams (Ross and Anderson 1990; Herman et al. 2003; Newton and Herman 2009) and permanent ponds (Graham and Butler 1993; Joyal et al. 2001; Beaudry et al. 2009; Refsnider and Linck 2012). Because turtles must maintain a cool body temperature to slow metabolism and conserve energy until spring (Edge et al. 2009), characteristics of suitable overwintering sites may include dissolved oxygen content (Dinkelacker et al. 2005; Ultsch 2006; Edge et al. 2009; Jackson and Ultsch 2010), substrate type (Greaves and Litzgus 2007), vegetation cover (Millar and Blouin-Demers 2011), and/or water temperature (Edge et al. 2009).

Given the many types of habitats used across the range of Blanding's Turtles, the only generalization that can be made is that individuals tend to overwinter in wetlands or areas of standing water. Not all wetlands are suitable overwintering habitats, however, and there is little field information that points to critical environmental requirements that must be included to make the habitat suitable beyond identification of occupied habitat types (Kofron and Schreiber 1985; Kiviat 1997; Hartwig and Kiviat 2007; Millar and Blouin-Demers 2011). Some conservation plans require confirmation of overwintering sites before sites can be designated as a sensitive area with low tolerance to alterations (Ontario Ministry of Natural Resources and Forestry 2013). Otherwise, sites that may be suitable but that do not have confirmed occupancy could be exposed to harmful alterations or activities. Furthermore, without more detailed knowledge regarding suitable overwintering habitats, recovery strategies that rely on creation or restoration of overwintering habitats do not have the specific criteria necessary to ensure habitats are suitable.

Even though little is known about the specific tolerance ranges of adult Blanding's Turtles *in situ*, oxic and thermal parameters of the water body are likely the largest contributors to overwintering site suitability (Ultsch 2006; Edge et al. 2009). Blanding's Turtles are considered anoxia tolerant because they often share overwintering sites with the Painted Turtle (*Chrysemys picta*) and Snapping Turtle (*Chelydra serpentina*), species known to be anoxia tolerant (Dinkelacker et al. 2005; Ultsch 2006). Under anoxic conditions, energy is produced through anaerobic respiration that can lead to the accumulation of lactic acid, but which can be buffered by release of carbonates stored in the shell (Dinkelacker et al. 2005; Jackson and Ultsch 2010). Nevertheless, excessive accumulation of lactic acid can result in metabolic acidosis and death when turtles are exposed to low oxygen conditions for an extended period of time (Dinkelacker et al. 2004; Jackson and Ultsch 2010). Given that Blanding's Turtles have been found to tolerate anoxic conditions (Edge et al. 2009; Newton and Herman 2009), temperature is likely more important than the level of dissolved oxygen in determining the suitability of a site. Temperatures, however, do not have to be above freezing consistently because the equilibrium freezing point for turtle body fluids is approximately -0.6° C (Costanzo et al. 2006). An ideal overwintering site should therefore have sufficiently cool temperature that will reduce the metabolism of the turtle but not so cold that the entire water column freezes.

With the large number of aquatic bodies throughout different landscapes in Ontario, Canada, and considering competing land uses, it would be beneficial for managers to identify and protect the most critical wetlands within their jurisidictions. Rather than focusing on the type of aquatic habitat per se, the goal of our study is to determine the thermal characteristics of occupied overwintering habitats within three populations of Blanding's Turtles in Ontario, Canada. Our primary objective is to use *in-situ* water temperature data to characterize suitable temperatures at occupied overwintering habitats. Determining thermal parameters suitable for overwintering is one step towards more thoroughly understanding where turtles overwinter and may provide a cost-effective framework to filter out unsuitable areas so that occupied habitats can be further evaluated with field surveys.

Materials and Methods

Study sites.—Our study was conducted in southern Ontario, Canada, with study areas located along the southeastern shore of Georgian Bay (northern study area), the northern shore of Lake Erie (southern study area), and a central study area located south of Georgian Bay, Lake Huron (Fig. 1). We selected these three study areas because they encompass a variety of different aquatic habitat types occupied by Blanding's Turtles, and reflect the potential range of thermal regimes experienced across southern Ontario (study areas range between 42.2° and 45.2° latitude). Within each study area, we monitored aquatic habitat types found within the core range of the local population of Blanding's Turtles. In the northern study area, we monitored four main aquatic habitat types including a coastal marsh, two bogs (east and west), and a vernal pool (Fig. 1). There are other vernal pools located in this landscape, but the particular pool we monitored was frequented by Blanding's Turtles in the springtime. It was also one of the few vernal pools to remain flooded during the winter study period, allowing us to monitor changes in water temperature. We analyzed the two bogs separately because they are distinct water bodies with unique physical attributes that may result in differences in water temperatures relevant to overwintering. For example, the East bog was significantly shallower with greater *Sphagnum* mat coverage compared to the West bog (Markle and Chow-Fraser 2014). In our southern study area, we monitored four aquatic habitat types: an open pool within a cattail marsh (herein referred to as South marsh pool), an open-water channel (herein referred to as open water), and two impounded wetlands (North and South; Fig. 1). The impounded wetlands were treated as separate habitat types because of differences in depth and vegetation cover and structure that may impact winter water temperature. The South impoundment is shallower, has more vegetation cover, and is dominated by dense cattails; whereas, the North impoundment has more open water and is dominated by graminoids. At our central study area, we monitored five aquatic habitat types, which included a string fen, thicket swamp, deciduous swamp, coniferous swamp, and a river (Fig. 1).

Blanding's Turtle locations.—We radio tracked adult Blanding's Turtles to identify occupied overwintering habitats. Any habitat that was occupied by one of the tagged turtles was considered confirmed overwintering habitat, while all others were considered unconfirmed. We used these designations solely to determine if sites occupied by radio-tagged Blanding's Turtles have thermal characteristics that are different from those of unconfirmed sites. In our northern study area, we radio tracked 12 individuals (six males, six females) in 2011 and an additional three turtles (two males, one female) in 2012 as part of another study (15 total; See Markle and Chow-Fraser 2014 for detailed tagging methods). Turtles were radio tracked on three dates during the

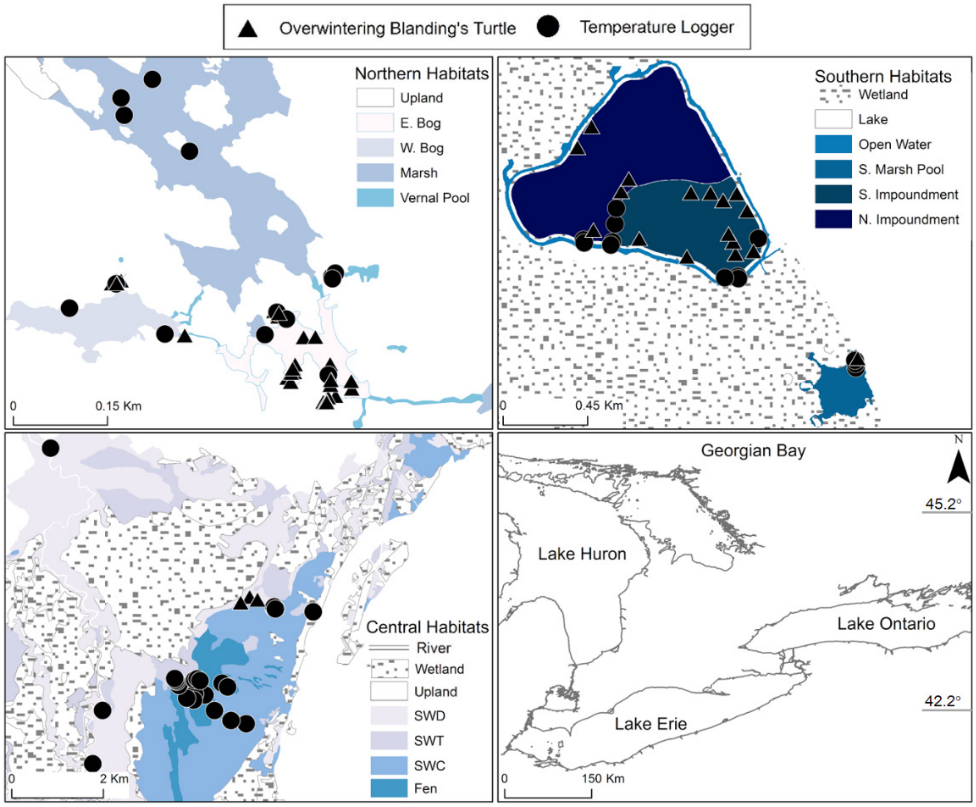

Figure 1. The southern, central, and northern study areas for Blanding's Turtles (*Emydoidea blandingii*) are distributed between 42.2° and 45.2° latitude in Ontario, Canada. Locations of our aquatic temperature logger sites (closed circles), overwintering Blanding's Turtles (triangles), and habitat types are shown for each study area. We monitored four aquatic habitat types (E. Bog, W. Bog, Marsh, Vernal Pool; 12 logger sites) in our northern study area, four aquatic habitat types (Open Water, S. Marsh Pool, S. Impoundment, N. Impoundment; 12 logger sites) in our southern study area, and five aquatic habitat types (River, Fen, Coniferous Swamp (SWC), Deciduous Swamp (SWD), and Thicket Swamp (SWT); 22 logger sites) in our central study area.

winter season (19 November 2011, 24 February 2012, and 19 February 2013; Fig. 1). In the southern study area, we radio tracked 30 Blanding's Turtles (15 males, 15 females) and identified their overwintering sites on 6 November 2014 (Fig. 1) and confirmed sites in April 2014 and 2015. The central study area was very difficult to sample because of the rugged terrain; therefore, we radio tracked only three females and no males. On 31 October 2014 and 3 April 2015, we tracked the females in the central study area to identify overwintering sites (Fig. 1).

Temperature data.—We used Tidbit v2 temperature loggers (HOBO Onset, Bourne, Massachusetts, USA) to monitor water temperatures of 13 potential overwintering habitat types across our three study areas (Fig. 1). We randomly selected sites for aquatic logger deployment using ArcGIS 10.2 (Esri, Redlands, California, USA) and set loggers to record water temperature every four hours. In some instances, water depth (> 1 m) and access prevented us from deploying loggers in the previously selected sites; therefore, we placed loggers as close to their randomly selected site as possible. We also installed three loggers within each study area to measure winter air temperatures (nine air sites total). We placed three loggers in 12 of the aquatic habitat types, and 10 loggers in the large continuous string fen complex in the central study area because of the large variety of suspected microhabitats. In total, we deployed temperature loggers at 46 aquatic sites (see logger sites in Fig. 1). We deployed temperature loggers from 21 September 2012 until 27 May 2013 at our northern site, from 7 November 2014 until 9 April 2015 at our southern site and from 30 October 2014 until 3 April 2015 at our central site.

Across all study areas, we mounted loggers used to monitor water temperature on rebar and placed them 7 cm above the substrate surface to approximate the location of an overwintering turtle, as outlined by Edge et al. (2009). We mounted loggers used to monitor air temperature on trees, 150 cm above the ground and shaded. Exclusive to the northern site, we set-up a Bushnell Trophy Camera XLT (model 119466CN; Bushnell Corporation, Overland Park, Kansas, USA) at the East bog to capture daily photographs to monitor the timing of onset and breakdown of ice cover during the 2012/2013 season.

Analyses.—We used a Spearman's correlation test (JMP v12; SAS Institute Inc., Cary, North Carolina, USA) to determine significant correlations among temperature datasets collected from loggers deployed within the same habitat type and study area. We pooled data from loggers deployed within the same habitat type and study area if $\rho > 0.6$. If temperature data were not correlated, we treated each independently to represent a unique thermal microhabitat within the larger aquatic habitat type (Table 1). We compared differences in mean water temperatures between confirmed and unconfirmed overwintering habitats using either non-parametric (Mann-Whitney U) or parametric (*t*-tests) tests as appropriate. We also tested for differences among air temperatures at our northern, southern, and central study areas using a Kruskal-Wallis one-way ANOVA and Steel-Dwass post-hoc tests. Lastly, we conducted a break-point analysis in R 3.2.1 to define periods of change in the water temperature data (R Core Team 2015). Because data for the three study areas had been collected during different winters (northern in 2012/2013, and the central and southern in 2013/2014), we used a break-point analysis to statistically delineate pre-overwintering, overwintering and post-overwintering periods rather than use calendar dates to do this because we did not know if there were interannual differences in onset of freezing and thawing. For all statistical tests, $\alpha = 0.05$.

We used water temperature data associated with occupied habitat types to characterize suitable overwintering temperatures in two ways. First, we calculated mean water temperature during the pre-overwintering and overwintering periods. Second, we calculated the rate of water temperature change during the overwintering period to quantify the pattern of cooling or warming. To define the suitable range for each criterion, we calculated 95% confidence intervals of the mean for each occupied habitat type. We evaluated each habitat type and selected the lowest and highest temperatures estimated from the 95% confidence intervals. We used the selected temperatures to form a conservative definition of suitability for each criterion.

Results

Overwintering sites.—Turtles in our northern study area overwintered in the two large bogs, and were not found in the coastal marsh or vernal pool. Individuals in the southern site occupied both impoundments and the South marsh pool during the overwintering period,

Table 1. Lowest average water temperature experienced during the Blanding's Turtle (*Emydoidea blandingii*) overwintering period in each habitat type monitored in Ontario, Canada. Logger Unit # identifies the specific loggers averaged for the analysis. Longest duration refers to the number of hours that the temperature at a site dropped below 0° C.

Study Area	Aquatic Habitat Type	Logger Unit #	Lowest Average Temp (° C)	Longest Duration (h)	BLTU Occupancy
Northern	East Bog	1, 2, 3	2.39		Confirmed
	West Bog	1, 2, 3	0.05		Confirmed
	Marsh	1, 2, 3	-10.03	8	Unconfirmed
	Vernal Pool	1, 2, 3	-0.07	20	Unconfirmed
Southern	Open Water A	1	3.20		Unconfirmed
	Open Water B	2, 3	1.74		Unconfirmed
	South Impoundment	1, 2, 3	0.50		Confirmed
	North Impoundment	1, 2, 3	0.38		Confirmed
	South Marsh Pool	1, 2, 3	0.35		Confirmed
Central	Fen A	1, 5, 9	-0.01	12	Unconfirmed
	Fen B	2, 6, 7, 8	-2.04	1840	Unconfirmed
	Fen C	3	-1.27	40	Unconfirmed
	Fen D	4	-0.03	116	Unconfirmed
	Fen E	10	-1.79	2148	Unconfirmed
	Coniferous Swamp A	1	-1.67	1208	Unconfirmed
	Coniferous Swamp B	2	0.00		Unconfirmed
	Coniferous Swamp C	3	-10.62	1820	Unconfirmed
	River	1, 2, 3	-0.58	16	Unconfirmed
	Thicket Swamp	1, 2, 3	-1.83	1184	Unconfirmed
	Deciduous Swamp	1, 2, 3	-0.33	196	Confirmed

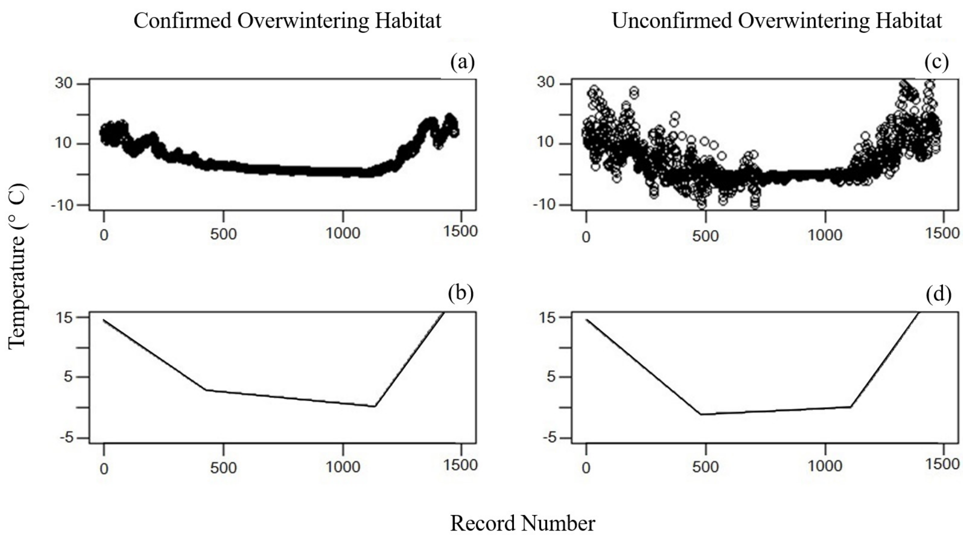

Figure 2. Example of typical changes in water temperatures (logged every 4 h) through the fall and winter months corresponding to habitats with (a) confirmed and (b) unconfirmed occupancy of Blanding's Turtles (*Emydoidea blandingii*) in Ontario, Canada. Best fit lines through the same temperature data after performing a break-point analysis identify the pre-overwintering, overwintering and post-overwintering periods and change in temperature for habitats with (c) confirmed and (d) unconfirmed occupancy.

and none were found overwintering in the open water channel. All three female Blanding's Turtles in our central study area overwintered in the deciduous swamp.

In the northern and southern study areas, we found no evidence of males and females using different overwintering habitats. Exclusive to the northern site, however, Blanding's Turtles overwintered in groups of two or three individuals where turtles were within 10 m of each other (11 groups during the 2011/2012 winter and seven groups during the 2012/2013 winter). Because we radio tracked 12 turtles in the northern study area for two consecutive winters (the additional three turtles were only tracked for one season), we were able to confirm site fidelity; 11 of the 12 individuals overwintered in the same habitat type, within 2–25 m of the location from the previous year. Remarkably, 11 of the 15 turtles overwintered in the East bog and experienced 99 d of continuous ice cover (21 December 2012 until 29 March 2013).

Temperature data.—Our three study areas included 13 different aquatic habitat types (Fig. 1). For 10 habitat types, temperature data from the three loggers within each habitat type were significantly correlated and were pooled. Except for the open-water habitat in the southern study area, one of the three loggers deviated from the other two and was treated as a different microhabitat type (Open Water A and B; Table 1). About a third of the loggers placed in the central study area yielded temperature data that were statistically unique and were treated as microhabitats (Fen A-E; Coniferous Swamp A-C; Table 1). The string fen spans over 3.5 km at its maximum length and provides both open water and densely vegetated microhabitats. After accounting for temperature correlations among logger sites, we were left with 20 potential overwintering habitat types that provided a unique thermal regime (see Table 1).

Onset and duration of the overwintering period were consistent among sites, beginning in November and ending in April, lasting between 133 and 147 d (Table 2; Fig. 2). There were among-site differences in air temperatures during the overwintering season (H = 72.12, $P < 0.001$); mean air temperature at the northern (-2.78° C) and southern (-2.19° C) study areas were not significantly different (Z = -1.17, P = 0.471), but they were both warmer than that monitored at the central (-5.52° C) study area (Z = -6.64, $P < 0.001$ for south vs. central; Z = -7.97, $P < 0.001$ for north vs. central). During the overwintering period, air temperature ranges were fairly equivalent among sites (northern site, 18° C to -29° C; southern site, 19° C to -30° C; central site, 19.5° C to -37° C).

We analyzed water temperatures separately for each of the study areas to elucidate differences between confirmed and unconfirmed overwintering habitats (Fig. 3). In the northern study area, water temperature of confirmed (2.68° C) overwintering habitats was warmer than that of unconfirmed (-0.07° C) habitats (Z = -43.3, $P < 0.001$; Fig. 3). A similar result was observed in the central study area (confirmed [1.00° C] vs. unconfirmed [0.15° C]; Z = 22.9, $P < 0.001$; Fig. 3). The opposite was true, however, for the southern study area; mean water temperature of confirmed (0.54° C) overwintering habitats were cooler than that of unconfirmed (4.08° C) habitats (Z = -36.6, $P < 0.001$; Fig. 3). Average water temperature of five of the six

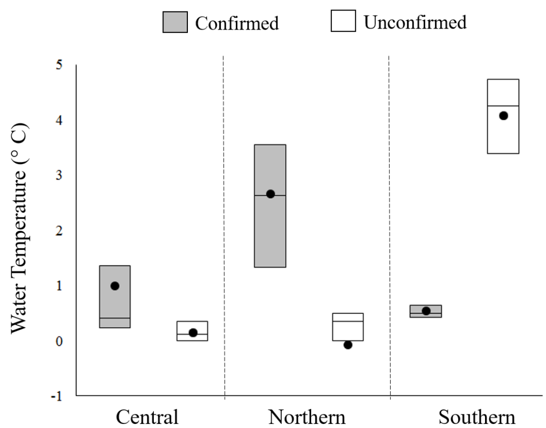

Figure 3. Mean water temperatures during the overwintering period in our central, northern, southern study areas for habitats with confirmed or unconfirmed occupancy of Blanding's Turtles (*Emydoidea blandingii*) in Ontario, Canada. Box plots are the central 50% of the data. The three horizontal lines of the box plots represent quantiles (25%, 50%, and 75% of the distribution). The closed circle is the mean value.

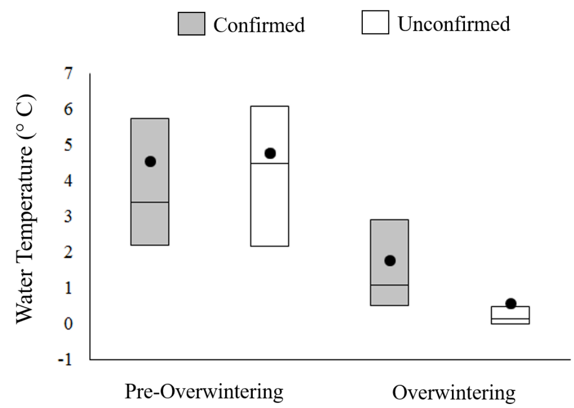

Figure 4. Mean water temperatures in confirmed and unconfirmed overwintering habitats during the pre-overwintering and overwintering periods of Blanding's Turtles (*Emydoidea blandingii*) in Ontario, Canada. Box plots are the central 50% of the data. The three horizontal lines of the box plots represent quantiles (25%, 50%, and 75% of the distribution). The closed circle is the mean value.

confirmed overwintering habitats never dropped below 0° C during the overwintering period (Table 1). The only confirmed overwintering habitat with average water temperature below 0° C was the deciduous swamp in the central study area (-0.33° C for 8 d). Furthermore, the lowest water temperature recorded by an individual logger in occupied habitat was in the East bog (northern study area) where water temperature was -0.62° C for fewer than 8 h. Also in the East bog, on two additional occasions, we recorded water temperatures below 0°C, both events lasting fewer than 8 h.

To assess differences between confirmed and unconfirmed overwintering habitat types at the landscape scale, we pooled temperature data across all three study areas. During the pre-overwintering period, mean water temperature at occupied habitats was slightly cooler (4.54° C) than that at unconfirmed habitats (4.77° C; $Z = 5.35$, $P < 0.001$; Fig. 4). On the contrary, during the overwintering period, mean water temperature at occupied habitats (1.77° C) was warmer than that at unconfirmed habitats (0.58° C; $Z = 50.27$, $P < 0.001$; Fig. 4). We tested for significant differences in rate of change in water temperature (pattern of cooling) during the pre-overwintering and overwintering period. We saw no difference in slopes between confirmed (-0.02) and unconfirmed (-0.08) habitat types during the pre-overwintering period ($Z = 1.36$, $P = 0.17$). During the overwintering period, we found that water temperature decreased by 0.50° C every six weeks; whereas, at unconfirmed habitats, water temperature increased by 0.25° C every six weeks ($t = 2.44$, df = 18, $P = 0.019$). Because rate of change in temperature (slope) is a single value per habitat type, we used the smallest and largest slopes to define the suitable range. Based on rate of temperature change at each study area, water temperatures in suitable habitats decline at a slow steady rate of -0.25° C to -1.3° C every six weeks.

We determined that suitable water temperature during the pre-overwintering period can range between 2.33° C and 10.22° C and between 0.44° C and 3.68° C during the overwintering period (Table 3). Additionally, we calculated the variance and range in suitable temperature during the pre-overwintering and overwintering periods. For occupied habitats, temperature variance was higher in the pre-overwintering (12.6° C) season than in the overwintering (2.25° C) season; similarly, the range in temperature was higher during the pre-overwintering (20.83° C) than in the overwintering (7.60° C) period (Table 3). Occupied habitats provided stable water temperatures during the overwintering periods, despite air temperatures dropping below -29° C.

Discussion

Our study used *in-situ* water temperature data from confirmed and unconfirmed overwintering habitats to characterize thermal suitability of overwintering habitat for the Blanding's Turtle. For purposes of habitat protection and restoration, field data are most appropriate but are not always available or easily attainable. Across our three study sites, Blanding's Turtles overwintered in water bodies with an average water temperature of 1.77° C (± [SE] 0.03° C), which was significantly warmer than that of unoccupied sites (0.58° C ± 0.01° C). This finding is opposite to that by Edge et al. (2009) where Blanding's Turtles in Algonquin Park were found occupying sites with water temperature cooler than what was generally available. That said, based on

Table 2. Comparison of dates marking the beginning and end of overwintering periods for three populations of Blanding's Turtles (*Emydoidea blandingii*) in Ontario, Canada. Duration of consistent ice cover was ascertained from daily photographs taken of the East bog.

Study Area	Overwintering Start Date	Overwintering End Date	Duration of Overwintering Period	Duration of Consistent Ice Cover
Northern	9 November 2012	3 April 2013	147 d	99 d
Southern	14 November 2014	3 April 2015	140 d	—
Central	23 November 2014	9 April 2015	133 d	—

temperature data measured at occupied habitat types across all study areas, suitable overwintering water temperatures ranged between 0.44° C to 3.68° C, similar to the range between 1.0° C to 3.0° C reported by Edge et al. (2009). Taken together, it appears that Blanding's Turtles overwinter in habitat types with a specific water temperature regardless of whether warmer or colder water temperatures are available. Water temperature data collected at additional overwintering habitats in Ontario would be useful in confirming these findings because a population of Blanding's Turtles in Nova Scotia overwintered in water temperatures that had a much larger range (0.3° C to 7.6° C; Newton and Herman 2009), and there was no evidence that turtles selected overwintering sites based on water temperature (Newton and Herman 2009).

Consistent with other studies (Litzgus et al. 1999; Newton and Herman 2009), we confirmed that overwintering water temperatures were stable (variance of 2.25° C), even though air temperatures were highly variable and dropped as low as -37° C. Our final *in-situ* thermal characteristic, rate of temperature change, differed significantly among habitats with confirmed and unconfirmed occupancy. In all occupied habitats, water temperature slowly decreased throughout the overwintering period (-0.5° C every six weeks). The steady decline in water temperatures may be energetically favourable and permit turtles to maintain an optimally low and stable body temperature as opposed to water temperatures in unoccupied habitats that slowly increased throughout the overwintering period (0.25° C every six weeks). Field studies in Ontario, Canada, have shown that a stable body temperature of just above 0° C is maintained by overwintering Blanding's Turtles (Edge et al. 2009), Spotted Turtles (*Clemmys guttata*; Litzgus et al. 1999; Rasmussen and Litzgus 2010) and Wood Turtles (*Glyptemys insculpta*; Greaves and Litzgus 2007). Although we did not measure the shell temperature of tagged Blanding's Turtles, Rasmussen and Litzgus (2010) found that Spotted Turtle shell temperature was not significantly different from water temperature recorded in occupied overwintering habitats. Therefore, our water temperature data are likely a close approximation to turtle shell temperature.

Considering the overwintering duration of the Blanding's Turtles in Algonquin Park was between 101

Table 3. Mean pre-overwintering and overwintering water temperatures (Temp; ° C) calculated for each of the habitat types where Blanding's Turtles (*Emydoidea blandingii*) occupancy was confirmed in Ontario, Canada. For each parameter, the most conservative confidence limit values were chosen to define the lower and upper boundaries of mean suitable temperature. We also indicate variance and range of suitable water temperature (° C) during the pre-overwintering and overwintering periods.

Parameter	Study Area	Aquatic Habitat Type	Mean Temp	Lower Mean Confidence Limit (95%)	Upper Mean Confidence Limit (95%)	Mean Suitable Temp	Suitable Variance	Suitable Range
Pre-Overwintering Water Temp	Northern	East Bog	9.80	9.37	10.22	2.33 to 10.22	12.60	20.83
		West Bog	8.62	8.28	8.97			
	Southern	S. Impoundment	3.02	2.92	3.11			
		N. Impoundment	3.11	2.96	3.26			
		S. Marsh Pool	2.46	2.33	2.59			
	Central	Deciduous Swamp	5.98	5.47	6.48			
Overwintering Water Temp	Northern	E. Bog	3.62	3.55	3.68	0.44 to 3.68	2.25	7.60
		W. Bog	1.58	1.52	1.65			
	Southern	S. Impoundment	0.70	0.69	0.71			
		N. Impoundment	0.45	0.44	0.45			
		S. Marsh Pool	0.48	0.47	0.49			
	Central	Deciduous Swamp	1.00	0.90	1.11			

and 136 d (Edge et al. 2009) and ours was between 133 to 147 d, this species appears to overwinter for 3.5–5 mo in Ontario, Canada. The Blanding's Turtles that overwintered in the East bog (northern study area) were under continuous ice cover for 99 d (confirmed through time-lapse photography), which is longer than the 87 d that Blanding's Turtles spent in anoxic conditions in Wisconsin (Thiel and Wilder 2010). Together, these data strongly support the hypothesis that Blanding's Turtles are anoxia tolerant, as suggested by Ultsch (2006), Edge et al. (2009), and Newton and Herman (2009) because ice cover would require turtles to remain submerged underwater without access to aerial oxygen. Blanding's Turtle's ability to survive prolonged periods of hypoxic or anoxic conditions suggest that dissolved oxygen conditions are not a major selection criterion of overwintering habitats, and indicates that water temperature is the primary selection criterion for the Blanding's Turtle.

At our northern site, both bogs and the vernal pool maintained sufficiently warm water temperatures above the freezing point of turtle body fluids (-0.6° C); but, only the bogs were used for overwintering. The lowest temperature recorded by an individual aquatic logger was -0.62° C in the East bog, a habitat that was used by majority of our tagged turtles in two consecutive winters. Although this sub-zero temperature lasted fewer than 8 h, these data lend support that adult Blanding's Turtles can survive in water temperatures of -0.6° C at least temporarily. It is possible that other untagged Blanding's Turtles overwintered in vernal pools because water temperature was sufficiently warm; however, this population is small and was extensively surveyed. Therefore, it is more likely that the habitat was unsuitable based on other criteria. For example, in all study areas, sites used for overwintering were characterized by organic muck, deep enough to allow complete burial of the turtle. Although we were unable to confirm the overwintering position of our tracked turtles, the ability to bury in substrate may provide protection from predators and temporary escape from freezing; however, prolonged burial inhibits access to dissolved oxygen (Ultsch 2006; Greaves and Litzgus 2007; Edge et al. 2009). The trade-off between requiring shelter and dissolved oxygen may explain why Blanding's Turtles have been found either partially (Ross and Anderson 1990) or fully (Kofron and Schreiber 1985; Sajwaj and Lang 2000) buried in mud, or just on top of the substrate (Graham and Butler 1993). Deep substrate was not available in the vernal pool, which was characterized by a shallow leaf-litter bottom and would not permit easy burial or concealment; potentially limiting suitable overwintering sites.

In the southern study area, all habitat types had water temperatures above 0° C, deep, organic muck substrate, and vegetation cover; however, we did not confirm occupancy in the open-water channel. In this situation, it is highly plausible that untagged turtles were overwintering in at least some of the sites deemed suitable because the population of Blanding's Turtles in the southern area is very large (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2005). At the central site, however, 10 of the 11 aquatic habitats had water temperatures ranging from -0.01° C to -10.62° C with sub-zero temperatures lasting upwards of 90 d (Table 1). Water temperatures in many of these habitats are well below the freezing point of body fluids (-0.6° C) and likely do not provide sufficient overwintering habitat. The large string fen complex, however, had been suspected to provide overwintering habitat for Blanding's Turtles. While two fen sites (fen A, D) never dropped below -0.6° C, all sites in the string fen had a mean overwintering temperature that was below the range of temperatures we monitored at occupied sites. Instead, we identified the deciduous swamp as overwintering habitat, a habitat type that has been declining in this wetland complex (Rootham and Featherstone 2014). Although the river site was thermally suitable, we did not confirm its use by Blanding's Turtles. In this case, we suspect that there are untagged turtles overwintering in habitat types that we did not monitor, but given the expansive and difficult terrain of this study area, it would have been extremely difficult to locate and track additional turtles.

Blanding's Turtles, among other freshwater turtles, have been found overwintering in groups (Ross and Anderson 1990; Newton and Herman 2009) possibly to increase access to mates or due to lack of suitable overwintering sites (Gregory 1982). Communal overwintering was observed in Algonquin Park (Edge et al. 2009), Nova Scotia (Newton and Herman 2009), and Wisconsin (Ross and Anderson 1990), similar to our observation at the northern study area. Greater availability of thermally suitable overwintering sites within the southern study area may contribute to the observed lack of communal overwintering. Limited communal overwintering in southern turtle populations is common (Gregory 1982; Brown and Brooks 1994) except for Wood Turtles, where communal overwintering is more apparent in southern compared to northern populations (Greaves and Litzgus 2008). Although Blanding's Turtles usually do not wander in excess of 5 m from their overwintering site, longer movements appear to be correlated with warmer water temperature and vice versa (Newton and Herman 2009). During the 2011/2012 overwintering season, only one female Blanding's Turtle in the northern study area made winter movements. Between her tracked locations on 19 November 2011 and 24 February 2012, she moved 25 m. Additionally, one other individual was seen on

24 February 2012 with its head above the surface of the water, indicative of the ability of turtles to respond to stimuli (temperature, light, limited ice cover) during the overwintering season (Madsen et al. 2013)

To survive until spring time, turtles in Ontario must select overwintering sites that balance the risk of freezing, metabolic acidosis, and predation. Aquatic overwintering poses many risks to turtle survival, and increasing air temperatures and decreasing precipitation associated with global climate change may have negative ramifications on the suitability of overwintering sites. The predicted warmer winters and drier conditions will result in wetlands with warmer water temperatures, reduced ice cover and lower water levels (Flato and Boer 2001; Colombo et al. 2007). These factors can all impact turtle overwintering, especially for populations that exhibit site fidelity (e.g., Innes et al. 2008; Edge et al. 2009; Newton and Herman 2009; Thiel and Wilder 2010). If commonly used sites become unsuitable over time, and individuals are unable to locate new sites, large numbers of turtles can be lost from the population at once (Brooks et al. 1991). Some studies suggest that turtles may be able to shift to new overwintering sites, although the mechanism triggering this shift is largely unknown (McNeil et al. 2000; Herman et al. 2003).

Turtles living at the northern extent of their range already experience more variable and extreme climates compared to those living in more southern areas. When we analyzed the northern, central and southern water temperature data separately, Blanding's Turtles used sites differently compared to available temperatures. In the northern and central areas, Blanding's Turtles selected for warmer habitat compared to unconfirmed habitats (Fig. 3), whereas those in the southern population selected for cooler habitat compared to what was available (Fig. 3). Newton and Herman (2009) suggested that turtles living in more northern areas would be better able to adapt to changing climates; however, existing habitat loss combined with climate change provides a unique set of challenges for species with a long generation time, and may render them unable to adapt to sudden environmental changes (Heller and Zavaleta 2009). Future research should investigate changes in phenology attributed to climate change because there is the potential for dissociation between times when turtles emerge and when resources become available. With warmer winter temperatures and reduced ice cover, turtles may emerge multiple times throughout the winter season. Additional energy reserves would be required to allow turtles to move into and out of overwintering sites, but these may not be forthcoming if food resources are unavailable during the winter months. Another risk is the possibility that the turtles become stranded on land when air temperatures suddenly plummet and ice forms over the surface, leaving the turtle to freeze (Neill 1948).

The impacts of climate change on turtles are largely unknown, but we can improve population resilience with targeted wetland conservation, restoration, and creation. Managers and planners can record wetland water temperatures during the winter months as a cost-effective framework to determine and monitor suitable overwintering sites. Our study provides thermal characteristics which define suitable overwintering sites in Ontario, Canada. Based on these characteristics, we can begin to determine the structural requirements of the site necessary to provide suitable water temperatures. Parameters outlining suitable temperatures and additional research on the physical structure of suitable overwintering habitats can then help improve wetland restoration and creation projects to ensure they provide necessary overwintering refugia. As additional field data become available, temperature thresholds determined from *in-situ* research will have the greatest applicability for habitat conservation purposes, especially in the face of a changing climate. Determining thermal parameters suitable for overwintering is one step towards more thoroughly understanding where turtles overwinter and why, and can provide knowledge useful for habitat creation and ensuring current habitats continue to provide suitable overwintering conditions.

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