
Overwintering Habitats of a Northern Population of Painted Turtles (*Chrysemys picta*):
Winter Temperature Selection and Dissolved Oxygen Concentrations

Author(s): Njal Rollinson, Glenn J. Tattersall and Ronald J. Brooks

Source: *Journal of Herpetology*, Jun., 2008, Vol. 42, No. 2 (Jun., 2008), pp. 312-321

Published by: Society for the Study of Amphibians and Reptiles

Stable URL: <https://www.jstor.org/stable/40060516>

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/40060516?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Herpetology*

Overwintering Habitats of a Northern Population of Painted Turtles (*Chrysemys picta*): Winter Temperature Selection and Dissolved Oxygen Concentrations

NJAL ROLLINSON,¹ GLENN J. TATTERSALL,^{2,3} AND RONALD J. BROOKS¹

¹Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

²Department of Biological Sciences, Brock University, St. Catharines, Ontario, Canada L2S 3A1; E-mail: gtatters@brocku.ca

ABSTRACT.—We compared shell temperatures of Painted Turtles (*Chrysemys picta*) overwintering in two different ponds in Algonquin Park, Canada, over one winter. Movements under the ice occurred from late November into late December or early January, and based on thermal data, turtles were likely not buried in the substrate. Over the course of the winter, one pond became severely hypoxic, whereas the other remained more highly oxygenated. Turtles in the hypoxic pond exhibited significantly lower shell temperatures than did the turtles in the normoxic environment, despite significantly cooler average water temperatures in the normoxic pond. Painted Turtles submerged in normoxic water can assimilate O₂ through extrapulmonary means, and cutaneous O₂ uptake at low temperatures would significantly delay the onset of metabolic acidosis. Therefore, we suggest that, in the present study, turtles in the hypoxic environment likely could not assimilate O₂ cutaneously; thus, these individuals may have voluntarily selected low temperatures to delay metabolic acidosis and conserve energy stores for the active season. Our limited data suggest that Painted Turtles possess behavioral adaptations to detect and respond to aquatic hypoxia.

The range of the Painted Turtle (*Chrysemys picta*) extends further north than that of any other North American turtle (Ernst et al., 1994), and at the species' northern range limit, it must cope with long, severe winters. There are indeed several risks associated with overwintering in ponds, streams, and lakes, including the possibility of depredation (Brooks et al., 1991; Brown and Brooks, 1994), becoming frozen in the ice (St. Clair and Gregory 1990), and metabolic acidosis associated with submergence in hypoxic water (reviewed by Ultsch, 2006). However, if specific cues within a pond predict these risks, then individuals may select overwintering sites based on microhabitat characteristics. Although a great deal of important research has quantified overwintering environments of turtles (e.g., Brown and Brooks, 1994; Litzgus et al., 1999; Crocker et al., 2000; Greaves and Litzgus, 2007), logistical difficulties involved in monitoring these overwintering microhabitats have largely precluded any definitive conclusions regarding the degree to which overwinter site selection occurs. It is interesting, however, that in many populations, turtles overwinter communally (Brown and Brooks, 1994; Litzgus et al., 1999; Ultsch et al., 2000), and individual hibernacula sometimes share common abiotic characteristics (Greaves and Litzgus, 2007). This suggests that there can be specific aspects of an overwintering environ-

ment that are deliberately selected (Ultsch, 1989).

Both temperature and dissolved oxygen may be important factors involved in overwinter site selection. For example, when overwintering, Painted Turtles greatly depress their metabolic state (Jackson, 2002), particularly, but not exclusively, by lowering body temperature; this conserves energy and delays metabolic acidosis. Indeed, Painted Turtles also exhibit a remarkable tolerance of metabolic acidosis, which is associated with submergence in hypoxic water (Jackson and Heisler, 1982; Ultsch and Jackson, 1982; Jackson, 2000), but laboratory studies have shown that at 3°C, *C. picta* survive longer submerged in oxygenated water than in anoxic water (Ultsch and Jackson, 1982). This is likely because *C. picta*, and many other turtles, are able to take up oxygen by nonpulmonary means (Root, 1949; Gatten, 1980; Ultsch and Jackson, 1982; Jackson et al., 2004), and thus cutaneous oxygen uptake at low temperatures can also delay the onset of acidosis (Herbert and Jackson, 1985). Therefore, in addition to low temperatures, high levels of dissolved oxygen may be an important component of an ideal overwintering environment.

To our knowledge, no study on *C. picta* has compared overwinter temperature selection and dissolved oxygen regimes in multiple ponds, and this approach may provide insights into the factors affecting overwintering site selection in this species. In the present study, we monitored

³Corresponding Author.

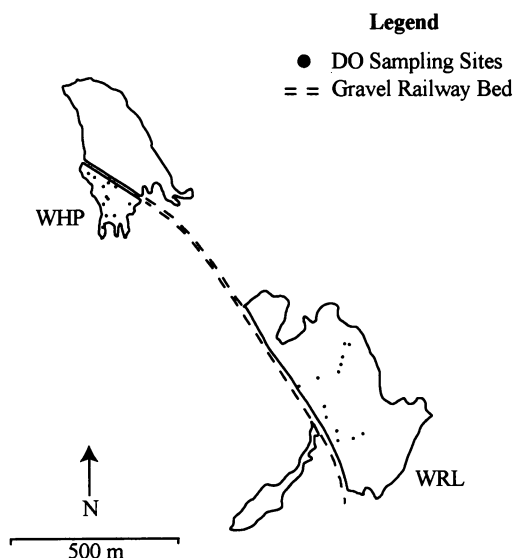


FIG. 1. Map of the study site, showing Wolf Howl Pond (WHP) and West Rose Lake (WRL). Small circles indicate the dissolved oxygen (DO) sampling sites during the winter ice cover.

overwinter shell temperature of Painted Turtles in two ponds while characterizing dissolved oxygen regimes and pond temperatures. Although we do not obtain information on the exact locations of turtles within these ponds, this comparative approach may nevertheless help elucidate proximate reasons for variation in temperature selection among ponds.

MATERIALS AND METHODS

Site Description.—This study is part of a larger life-history study that was initiated in Algonquin Provincial Park (45°34'N, 78°41'W) in 1978. Over 500 Painted Turtles are individually marked at our long-term study site. There are two ponds in which the vast majority of turtles reside. Wolf Howl Pond is a 1.70-ha black spruce (*Picea mariana*) bog that is predominantly 1.3 m deep and is bisected into an east and west side by a 4-m high railway embankment (Fig. 1). All turtles from WHP that were involved in this study overwintered on the west side. West Rose Lake (WRL) is located approximately 500 m southeast of WHP; it is larger in total surface area, and the railway embankment runs along its westernmost shore. Because WRL is larger, it is much more variable in depth; however the average depths of the two ponds are similar. WHP and WRL are not directly connected via streams or rivers, but a small stream empties into WRL on its eastern shore, and water levels in WRL are maintained by a beaver dam located on the western shore.

Both ponds are riddled with partially submerged stumps and logs, and there are numerous floating mats of Sphagnum, sedge (*Rhynchospora alba* and *Eleocharis smallii*), and leatherleaf (*Chamaedaphne calyculata*).

Monitoring Turtle Temperature.—Twelve sexually mature females from WRL and 11 mature females from WHP were caught in late August 2004. One DS1921Z iButton (resolution = 0.125°C, reported accuracy $\pm 1.0^\circ\text{C}$, Dallas Semiconductors, TX) programmed to read temperature at 190-min intervals (this interval ensured sufficient memory for the entire winter) was glued with Plumber's Sealant (Loctite, Inc.) to the aluminum field tag located on the posterior portion of each turtle's carapace. Turtles were released into their respective ponds and recaptured between 22 April and 30 May 2005. Because we recorded turtle and ambient temperatures every 190 min (see section below), we could use the absolute rate of temperature change ($^\circ\text{C h}^{-1}$) as an indicator of activity, assuming that stationary turtles would change temperature at similar rates to the microhabitat they had chosen, whereas active animals would move in and out of different thermal environments. This rate was calculated initially as the absolute rate of temperature change over 570-min periods of time (three times the sampling interval); subsequent daily averages were obtained and compared to similar rates calculated from iButtons recording water temperature within the ponds. Upon retrieval from the field, iButtons were calibrated against a NIST traceable temperature standard, and verified to be within 0.1–0.2°C of this standard, rather than 1°C as stated by the company.

Monitoring Environmental Temperature and Dissolved Oxygen.—In August 2004, we located the deepest point in WRL (1.75 m) and in WHP (1.40 m). We placed a wooden stake at the deepest point in each pond, and at specific locations along each stake (see results), we placed a tandem pair of DS1921G iButtons (Dallas Semiconductors, Dallas, TX) to record water temperature; five iButton pairs were attached to each stake, and the data from each iButton pair were later averaged to obtain a more reliable estimate of water temperature at each respective depth. We chose to place the stakes at the deepest point of each pond so that the entire range of temperatures available to overwintering turtles could be determined. All iButtons were programmed to read every 190 min, and these water temperature readings were synchronized with turtle temperature readings.

We also sampled dissolved oxygen and temperature profiles (separate from the iButton

measurements) in both ponds on 16 January, 6 February, 27 February, and 24 March 2005, using a YSI (Model 55) handheld dissolved oxygen and temperature meter (YSI, Inc., Yellow Springs, OH). Holes were drilled in the ice with an ice auger (diameter of each hole ~20 cm). To ensure our dissolved oxygen and temperature profiles were comparable between ponds, we used a stratified-random sampling method based on water depth. On each visit, we randomly selected one point on each pond from an area that was estimated to be 0–50 cm water depth, one point located in an area estimated to be 51–100 cm water depth, and one point estimated to be greater than 100 cm in depth (three profiles were taken per pond per visit). However, because water levels in WRL appear to have fluctuated over the winter (likely because of water influxes from the feeder stream and changes in the structural integrity of the beaver dam), all samples from WRL were taken at a depth of 100 cm or less (see Results, Table 1). Profiles were created by recording temperature and dissolved oxygen every 20 cm beginning at the ice-water interface and ending just before the mud-water interface.

Data Analysis and Statistics.—We used a repeated-measures ANOVA to test whether females differed in temperature selection among ponds. Shell temperatures of each turtle were averaged for each seven-day period between 29 November 2004 and 10 April 2005 (19 wk in total). Week was considered a within-subject factor ($N = 19$), pond of origin was a between-subject factor, and individual turtles were repeated subjects ($N = 22$). The coefficient of variation (CV) in temperature selection for females in both ponds was calculated for each 24-h period (spanning 28 November to 10 April). Statistical significance was considered

to be $P < 0.05$. Means are given ± 1 SD, unless otherwise indicated.

RESULTS

Thermal Stratification.—Unfortunately, because the stakes protruded above the surface of both ponds, ice formation both stripped some of the upper iButtons from the stakes and resulted in vertical movement of the stakes during the course of the winter. In the spring of 2005, iButtons in both WRL and WHP were located 45 cm lower than their original placement in the summer of 2004 (i.e., wooden stakes in both ponds were driven a further 45 cm into the mud during the winter of 2004–05). Four iButton pairs were retrieved from the stake at WHP: one iButton pair was situated 35 cm below the mud-water interface, and the three remaining pairs were 10 cm, 55 cm, and 65 cm above the interface. At WRL, the three remaining iButton pairs were located 55 cm and 10 cm below the mud-water interface and 35 cm above the mud-water interface. The degree of thermal stratification in each pond was approximated by the linear relationship between water temperature and water depth, using the final depth estimate (Fig. 2). A steeper slope is indicative of a more rapid change in temperature with increasing water depth (note that slopes have been multiplied by -1 for ease of interpretation). We assumed that high r^2 -values and slopes are indicative of ice formation on the ponds; low values are more likely to occur when ponds are not frozen over and convective vertical mixing can lead to variable temperature-depth relationships that disrupt the normal density-driven temperature-depth relationship. Thermal stratification appeared to be more pronounced in WHP, with temperature chang-

TABLE 1. Dissolved oxygen (DO) regime of WHP and WRL. Mean DO represents the mean DO concentrations across all three sampling profiles taken at each visit, and “mean sample depth” is the average depth of all samples (encompassing all three profiles) taken on each visit. “Slope” is the slope of DO over water depth.

	Ice depth (cm)	Min, Max water depth (cm) where profiles were taken	Mean (range) sample depth	Mean (range) DO (mg L ⁻¹)	Slope [SE] (mg L ⁻¹ cm ⁻¹)	r ²	N samples
WHP							
16 Jan	40–45	80, 140	80.0 (40–140)	4.06 (0.14–8.94)	−0.91* [0.022]	0.72	9
6 Feb	35–45	65, 115	64.0 (40–100)	2.08 (0.08–7.37)	−0.087* [0.034]	0.45	10
27 Feb	30–50	70, 120	70.9 (40–120)	0.529 (0.10–3.03)	−0.015 [0.010]	NS	11
24 Mar	50	90, 100	64.0 (40–100)	0.195 (0.07–0.41)	−0.004* [0.001]	0.54	10
WRL							
16 Jan	40	70, 110	54.2 (40–100)	12.3 (9.18–13.6)	−0.005 [0.032]	NS	7
6 Feb	40	65, 90	57.5 (40–80)	10.5 (5.20–12.8)	−0.105* [0.042]	0.51	8
27-Feb	30–50	60, 100	60.0 (40–100)	5.65 (0.32–11.4)	−0.035 [0.070]	NS	8
24-Mar	30–50	50, 90	54.3 (40–80)	9.25 (4.62–11.7)	−0.025 [0.072]	NS	7

* $P < 0.05$

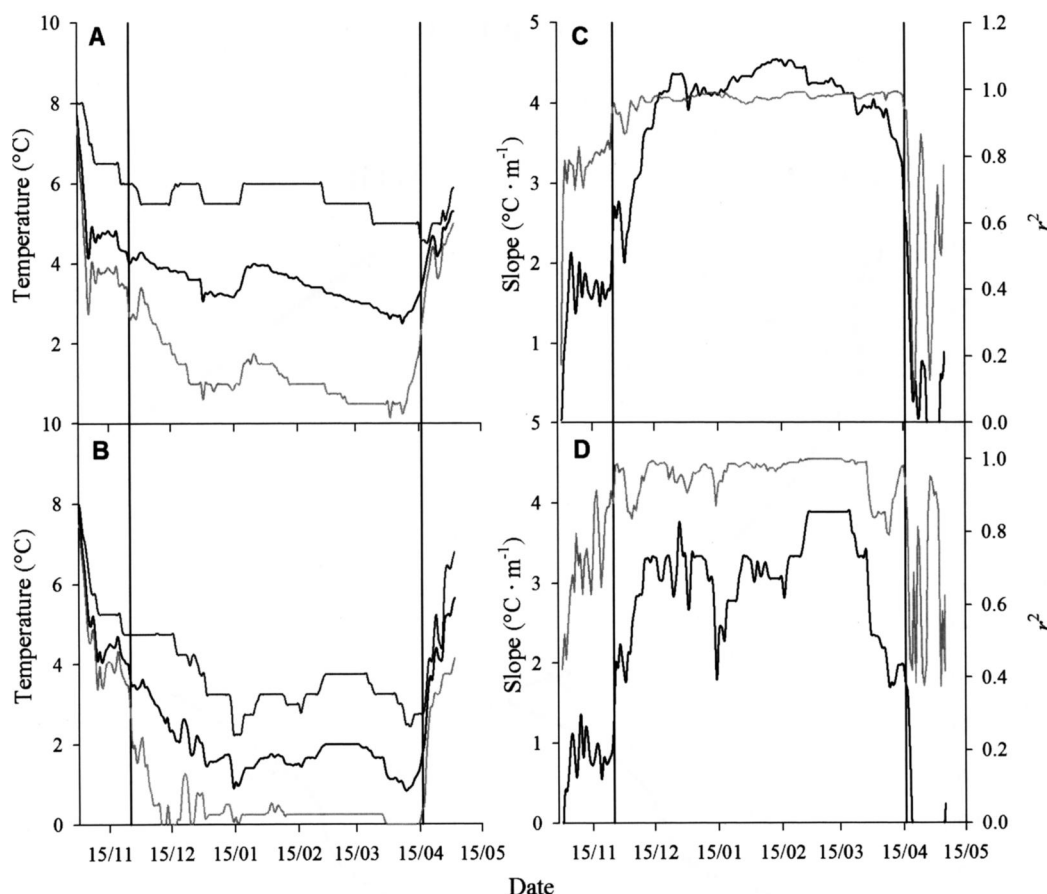


FIG. 2. Mean (black line), minimum (light grey), and maximum (dark grey) pond temperatures measured continuously from iButtons attached to stakes in WHP (A) and WRL (B). Slopes of the linear relationship between water depth and water temperature (dark lines) in WHP (C) and WRL (D) between 1 November and emergence are shown (slope values have been multiplied by -1). The corresponding r^2 -values (grey lines) in C and D represent the proportion of variation in temperature explained by depth. r^2 -values approached 1.0 when ice formation persisted, resulting in temperature becoming stratified with depth according to density-temperature relationships. Solid vertical lines indicate the times when ice would have been present on the water surface based on elevated slopes and r^2 -values.

ing more sharply with water depth (Fig. 2). There was also a greater range of available temperatures in WHP. Based on the Pearson's coefficients of temperature versus depth, ice appeared to have formed around 25 November, lasting until 16 April in both WHP and WRL. From 28 November to 10 April, the temperatures recorded 35 cm below the mud-water interface at the deepest point in WHP were between 5.0°C and 6.0°C (mean = $5.6 \pm 0.34^\circ\text{C}$), whereas the temperatures 55 cm below the mud-water interface at the deepest point in WRL ranged from 2.3–4.8°C (mean = $3.5 \pm 0.66^\circ\text{C}$) during the same period (Fig. 2). Finally, water temperatures measured while sampling the ponds (these temperature measurements were taken at randomly determined locations in conjunction with

dissolved oxygen profiles) were significantly higher in WHP (mean = $1.37 \pm 1.0^\circ\text{C}$, $N = 42$) than in WRL ($0.287 \pm 0.188^\circ\text{C}$, $N = 31$; Mann Whitney U -test, $Z = -6.22$, $P < 0.001$).

Dissolved Oxygen.—WHP experienced relatively low dissolved oxygen concentrations, compared to WRL (Fig. 3), but because of fluctuating water levels in WRL, sample depths were, on average, slightly deeper in WHP (Table 1). WHP exhibited a clear temporal decline in average dissolved oxygen concentrations, whereas no trend was evident in WRL. Finally, there was a greater propensity for dissolved oxygen concentrations to decline with sample depth at WHP, but this may be, in part, a result of the greater range of sample depths taken per profile taken at WHP (Table 1; Fig. 3).

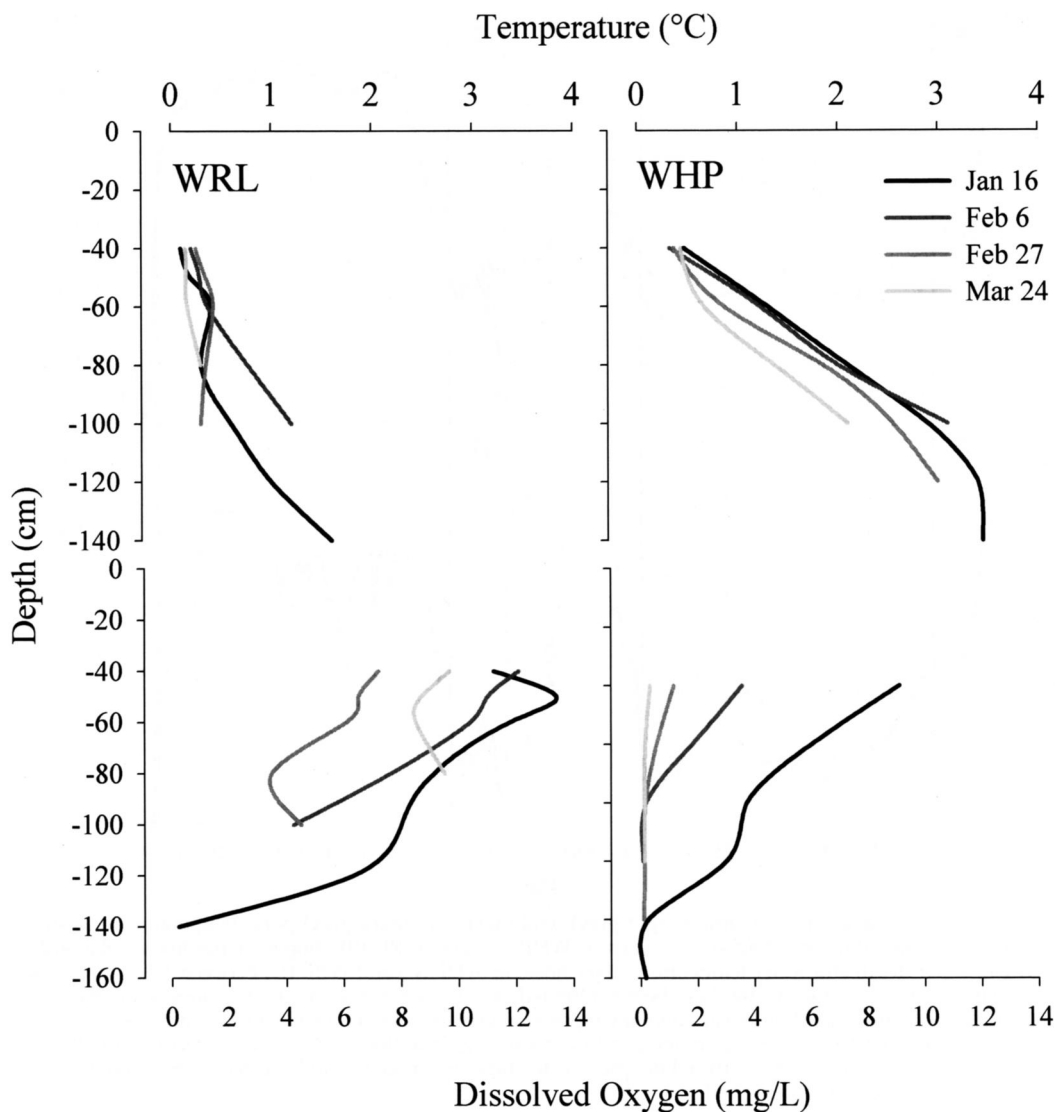


FIG. 3. Dissolved oxygen (DO) and temperature profiles of WHP and WRL on each sampling occasion from 16 January to 2 March. Values for specific depths were averaged for a given visit (i.e., all measurements taken at a depth of 60 cm were averaged within each pond).

Temperature Selection by Females.—For each day between 24 January and 10 April, a *Q*-test was performed to determine whether one of the females that selected relatively high temperatures qualified as an outlier. We found that the calculated *Q*-value invariably exceeded the critical *Q*-value for the entire period (range of calculated *Q*-values = 0.70–2.7, $Q_{crit} = 0.47$, $N = 10$, $\alpha = 0.05$); thus, this individual was considered an outlier and was omitted from our analyses. Based on thermal profiles of turtles (Fig. 4), females in WHP were likely submerged for at least 143 days (~ 28 November ~ 20 April), whereas submergence probably

lasted for at least 138 days (~ 28 November ~ 15 April) for females in WRL. Mean “selected” temperature decreased significantly over the 19 wk (Table 2), and the pond $\times$ week interaction term was not significant (although weakly so), indicating that the nature of the decrease in temperature selection between ponds (e.g., the timing and magnitude) was similar, and that WHP females maintained significantly lower shell temperatures throughout the winter. As an example, the daily average temperature of a turtle in WHP on 15 December was $0.69 \pm 0.45^\circ\text{C}$ compared to $1.54 \pm 1.11^\circ\text{C}$ in WRL. By 2 February, both groups exhibited the seasonal

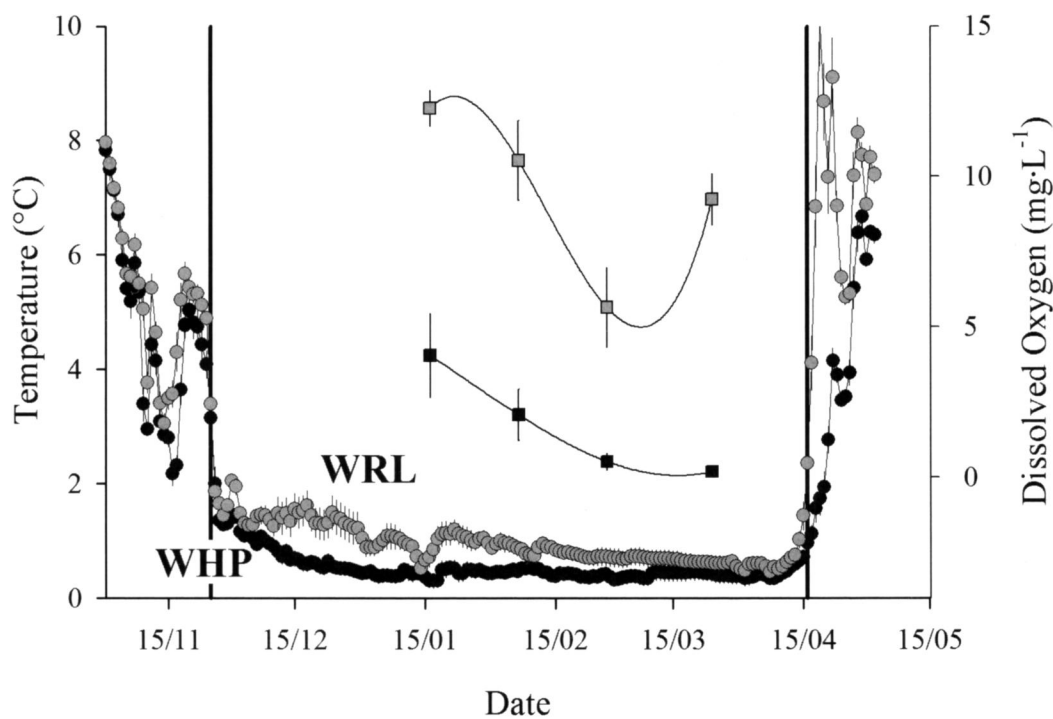


FIG. 4. Mean ($\pm$ SEM, for clarity) selected of females in WHP ($N = 10$) and WRL ($N = 12$) are depicted for each 24-h period between 1 November and emergence. Solid vertical lines indicate the times when ice would have been present on the water surface. Also shown are the mean ($\pm$ SEM) DO-values (squares; black, WHP; grey, WRL) measured during the months of February and March, showing the consistently higher oxygen levels in WRL than in WHP.

decline in temperature, with values of $0.44 \pm 0.43^{\circ}\text{C}$ in WHP and $0.68 \pm 0.51^{\circ}\text{C}$ in WRL. Females from WRL exhibited less variability in temperature selection (mean CV = $65.0 \pm 18.3\%$, $N = 12$ females) than females from WHP (CV = $82.7 \pm 24.3\%$, $N = 10$ females). This disparity was not pronounced in the first portion of the winter but became more pronounced as the winter progressed (Fig. 5).

The rate of turtle temperature change appears to have remained above the rates of water

temperature change until approximately the end of December 2004, with occasional periods of time with elevated rates of temperature change into the month of January 2005 (Fig. 6). From February until the surface ice melted, the rates of turtle temperature change appear not to differ from those of the water itself. No discernible difference appears to exist in the rates of turtle temperature change between ponds, excepting that it is apparent that temperatures of turtles and rates of temperature

TABLE 2. ANOVA results from the shell temperatures of turtles in the two ponds, WHP and WRL. We used a repeated-measures ANOVA to test whether females in WHP ($N = 10$) selected a lower temperature than females in WRL ($N = 12$). Shell temperature of each turtle ($N = 22$) was averaged for each seven-day period between 29 November 2004 and 10 April 2005 (19 wk in total). Week was considered a within-subject factor ($N = 19$), pond of origin was a between subject factor (WHP or WRL), and individual turtles were repeated subjects ($N = 22$). The assumption of sphericity was violated (Mauchly's $W < 0.001$, approximate $\chi^2 = 579.6$, $df = 170$, $P < 0.001$); hence, degrees of freedom are corrected using the Greenhouse-Geisser Epsilon.

	Type III SS	df	MS	F	P
Within subject effects					
Week	26.8	4.05	6.62	14.0	< 0.001
Week $\times$ Pond	3.96	4.05	0.980	2.07	0.092
Between subject effects					
Pond	19.8	1	19.8	6.46	0.019

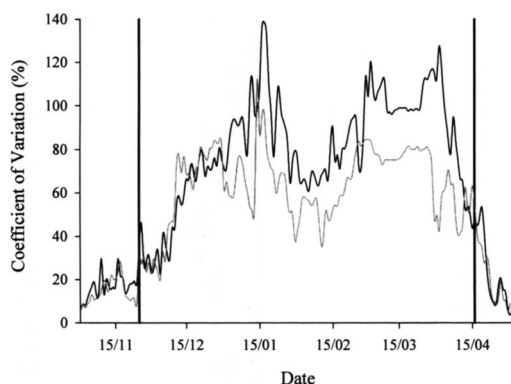


FIG. 5. Coefficient of variation in mean daily selected temperature among females (i.e., among-female variation) from WHP (black line) and WRL (grey line) from 1 November to emergence.

change in turtles from WRL increase days before those of WHP following the ice melt. For at least five days in the spring, WRL turtle temperatures exceed those from WHP, despite similar ambient temperature profiles between the two sites.

DISCUSSION

The incredible anoxia tolerance exhibited by *C. picta* has been emphasized by previous laboratory work (reviewed by Ultsch, 2006). However, our study suggests that these animals are not spending much of the winter submerged in anoxic mud. If that were the case, we would have observed much higher temperatures being selected by the turtles, given those microhabitats were available. Evidently, Painted Turtles are avoiding the deepest, most anoxic regions of their overwintering habitats (St. Clair and Gregory, 1990; but see Taylor and Nol, 1989). Moreover, turtles likely continued to move beneath the ice until late December or early January (Fig. 6), and it is possible that these early winter movements, which have also been documented in other studies (e.g., Gibbons, 1968; Taylor and Nol, 1989; Greaves and Litzgus, 2007), occurred because turtles were actively seeking appropriate overwintering locations.

We observed that turtles in WHP exhibited significantly lower temperatures than turtles in WRL, despite average temperatures in WRL being much lower. Also of note is that WHP became severely hypoxic over the course of the winter, whereas WRL remained relatively well oxygenated. Interestingly, this suggests that, when maintaining an aerobic metabolism was possible, females were selecting a micro-environment based primarily on dissolved oxygen and not necessarily temperature. Conversely,

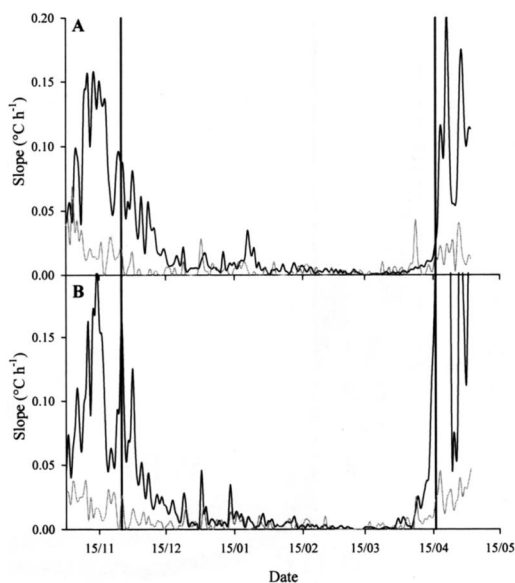


FIG. 6. Comparison of the daily absolute rate of shell temperature change ($^{\circ}\text{C h}^{-1}$) in turtles (black lines) from WHP (A) and WRL (B) with the daily average absolute rate of water temperature (grey lines) change ($^{\circ}\text{C h}^{-1}$). Solid vertical lines indicate the times when ice would have been present on the water surface. Rates of temperature change in the turtles higher than the rates at which water temperatures change would be indicative of movement by the turtles.

when maintaining an aerobic metabolism was not possible, females were selecting microhabitats based on (low) environmental temperature. However, in contrast to this conjecture, we observed a greater coefficient of variation in temperature selection among turtles in the hypoxic environment (Fig. 5), which would not be expected if turtles in the hypoxic environment were actively selecting a narrow range of (low) temperatures. It is possible that the increased variability in shell temperature reflects a reduction in behavioral thermoregulatory precision, as has been observed in laboratory studies on thermoregulation in hypoxia (Cadena, 2007). However, because we examined only two ponds, it is impossible to establish whether the observed patterns reflect chance, coincidental events, or whether turtles in the hypoxic pond actively selected relatively cool temperatures. Notwithstanding the limitations of this study, the data suggest that behavior of turtles overwintering in a hypoxic environment may differ from those overwintering in normoxic environments, and the possibility that Painted Turtles possess both physiological and behavioral adaptations to hypoxia certainly warrants further consideration.

It is likely that Painted Turtles can discriminate between normoxic and hypoxic environments (St. Clair and Gregory, 1990; Prassack et al., 2001). It will be interesting to establish whether Painted Turtles use thermal gradients in nature to manipulate metabolic expenditure and degree of acidosis, as even the small differences in turtle temperatures observed among environments (ponds) in the current study likely translate into moderate differences in energy expenditure (and possibly the degree of acidosis). On 15 December, for example, the difference in turtle temperature among ponds was $\sim 0.85^{\circ}\text{C}$. Based on data from overwintering turtles (Herbert and Jackson, 1985) where the Q_{10} can be as high as 8.5, this would translate into a 19% difference in metabolism between turtles at the two sites, although this disparity nearly disappeared by February, where the 0.2°C difference should have led to a 5% difference in metabolism. Although the energy stores of Painted Turtles are not thought to limit overwinter survival (St. Clair and Gregory, 1990; Ultsch, 2006), any energy conserved while overwintering could be diverted into growth and reproduction; thus, minimizing energy expenditure during the winter may be favored by selection. Indeed, submergence in normoxic water, which may delay acidosis, is also associated with higher metabolic rates in *C. picta* (Herbert and Jackson, 1985), so the benefit of delaying metabolic acidosis must also be weighed against the costs of an increased metabolic rate.

Several laboratory studies involving a variety of ectothermic species have shown that a voluntary reduction in preferred body temperature occurs under laboratory conditions (e.g., Wood and Malvin, 1991; Tattersall and Boutilier, 1997, 1999) and that the physiological benefits of reducing body temperature are manifested in delayed or reduced anaerobiosis, increased oxygen affinity, and a general preservation of aerobic metabolism (see also Jackson and Heisler, 1982; Ultsch and Jackson, 1982; Jackson, 2000). Laboratory studies on *Rana temporaria* (a frog that overwinters under the ice), for example, have shown that dissolved oxygen significantly influences the frogs' preferred environment (Tattersall and Boutilier, 1999); however, no studies have successfully documented the occurrence or importance of these phenomena in the field. The present results are encouraging, in that such responses in the laboratory may be observed under field conditions, although the overall low temperatures exhibited by the turtles in the present study obscures the potential importance of hypoxia-induced alterations in thermal preference in ectotherms. One intriguing possibility is that the extreme hyp-

oxemia exhibited even by turtles in normoxic water (Ultsch et al., 1999) is the driving force behind the low temperatures observed in both groups of turtles. If the hypoxia-induced decline in preferred temperature observed in laboratory studies (Wood and Malvin, 1991; Tattersall and Boutilier, 1997) is applicable to natural conditions, then a cold-submerged turtle in normoxic water is already experiencing internal hypoxia; these turtles might then be expected to aggregate toward the shallow, cooler waters as an inherent response to their internal hypoxia, making the possibility of detecting a difference in selected temperatures between a normoxic pond and an anoxic pond quite difficult. It is impossible to discount this possibility, although examining the overwintering thermal preferences in ectotherms that both rely on significant cutaneous gas exchange (soft-shelled turtles or skin-breathing amphibians) and that have much lower inherent tolerance to anoxia may yield different results. Such studies may help to resolve the question of whether hypoxia causes animals to select lower temperatures in nature.

It is evident in both populations of turtles that shell temperature declines throughout the period of submergence and that shell temperature is lower than the average pond temperature, despite a wide range of possible temperatures to select. Thus, regardless of oxygen levels in their environment, Painted Turtles appear to inhabit shallow, relatively cool environments throughout the winter, even though higher temperatures are still available in the deeper waters. Selecting cool temperatures to depress metabolic rates may be beneficial (both by conserving energy and delaying the onset of acidosis), as the energetic costs of overwintering may not be trivial (Crawford, 1994). However, there is also a degree of risk associated with this behavior. The lowest available temperatures are usually located at the ice-water interface; thus, selecting the coolest temperature available would increase the risk of becoming frozen in the ice or shallow mud, which would result in mortality. This risk would be especially pronounced in environments subject to fluctuating water levels, such as beaver ponds. Presumably, Painted Turtles have inhabited beaver ponds for many millennia. Thus, if the risk of mortality associated with selecting low environmental temperatures outweighs the benefits associated with voluntary hypothermia, this behavior would not have persisted. Notwithstanding, at least two studies report that Painted Turtles frequently overwinter close to shore on the mud surface (St. Clair and Gregory, 1990; Crocker et al., 2000), even though this behavior was clearly a mortality factor in one study (St. Clair and Gregory, 1990).

In sum, we found that overwintering temperature selection differed among Painted Turtles inhabiting environments with different dissolved oxygen regimes, although this observation warrants repetition at other sites with varying degrees of oxygenation and in other overwintering ectotherms with variable hypoxia tolerances. Although our data should not be considered first evidence of a behavioral adaptation to hypoxia, there are a variety of reasons to suspect that such adaptations may exist, given the wealth of laboratory data supporting such thermoregulatory responses. Similar endeavors in the future directed at testing such phenomena in the field may indeed prove fruitful.

Acknowledgments.—We would like to thank D. Reeves, J. Desroches, P. Rollinson, C. Rollinson, and J. Porter for their help collecting field data. This research was funded by NSERC grants to R. J. Brooks, N. Rollinson, and G. Tattersall. Animal handling was authorized by the University of Guelph Animal Care Committee (AUP04R053) and wildlife permits issued by the Ministry of Natural Resources, Algonquin Park.

LITERATURE CITED

- BROOKS, R. J., G. P. BROWN, AND D. A. GALBRAITH. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common Snapping Turtle (*Chelydra serpentina*). *Canadian Journal of Zoology* 69:1314–1320.
- BROWN, G. P., AND R. J. BROOKS. 1994. Characteristics of and fidelity to hibernacula in a northern population of Snapping Turtles, *Chelydra serpentina*. *Copeia* 1994:222–226.
- CADENA, V. 2007. Level and Precision of Behavioural Thermoregulation in the Bearded Dragon, *Pogona vitticeps*: Effects of Hypoxia and Environmental Thermal Quality. Unpubl. master's thesis. Brock University, St. Catharines, ON, Canada.
- CRAWFORD, K. M. 1994. Patterns of energy substrate utilization in overwintering Painted Turtles, *Chrysemys picta*. *Comparative Biochemistry and Physiology A* 109:494–502.
- CROCKER, C. E., R. A. FELDMAN, G. R. ULTSCH, AND D. C. JACKSON. 2000. Overwintering behaviour and physiology of eastern Painted Turtle (*Chrysemys picta picta*) in Rhode Island. *Canadian Journal of Zoology* 78:936–942.
- ERNST, C. H., J. E. LOVICH, AND R. BARBOUR. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, DC.
- GATTEN, R. E., JR. 1980. Aerial and aquatic oxygen uptake by freely diving Snapping Turtles (*Chelydra serpentina*). *Oecologia* 46:266–271.
- GIBBONS, J. W. 1968. Reproductive potential, activity, and cycles in the Painted Turtle, *Chrysemys picta*. *Ecology* 49:399–409.
- GREAVES, W. F., AND J. D. LITZGUS. 2007. Overwintering ecology of the Wood Turtle (*Glyptemys insculpta*) at the species' northern range limit. *Journal of Herpetology* 41:32–40.
- HERBERT, C. V., AND D. C. JACKSON. 1985. Temperature effects on the responses to prolonged submergence in the turtle *Chrysemys picta bellii*. II. Metabolic rate, blood acid-base and ionic changes, and cardiovascular function in aerated and anoxic water. *Physiological Zoology* 56:670–681.
- JACKSON, D. C. 2002. Hibernating without oxygen: physiological adaptations of the Painted Turtle. *Journal of Physiology* 543:731–737.
- JACKSON, D. C., AND N. HEISLER. 1982. Plasma ion balance of submerged anoxic turtles at 3°C: the role of calcium lactate formation. *Respiratory Physiology* 49:159–174.
- JACKSON, D. C., C. E. CROCKER, AND G. R. ULTSCH. 2000. Bone and shell contribution to lactic acid buffering of submerged turtles *Chrysemys picta bellii* at 3°C. *American Journal of Physiology—Regulatory, Integrative and Comparative Physiology* 278: 1564–1571.
- JACKSON, D. C., E. M. RAUER, R. A. FELDMAN, AND S. A. REESE. 2004. Avenues of extrapulmonary oxygen uptake in western Painted Turtles (*Chrysemys picta bellii*) at 10°C. *Comparative Biochemistry and Physiology A* 139:221–227.
- LITZGUS, J. D., J. P. COSTANZO, R. J. BROOKS, AND R. E. LEE. 1999. Phenology and ecology of hibernation in Spotted Turtles (*Clemmys guttata*) near the northern limit of their range. *Canadian Journal of Zoology* 77:1348–1357.
- PRASSACK, S. L., B. BAGATTO, AND R. HENRY. 2001. Effect of temperature and aquatic PO₂ on the physiology and behaviour of *Apalone ferox* and *Chrysemys picta*. *Journal of Experimental Biology* 204:2185–2195.
- ROOT, R. W. 1949. Aquatic respiration in the musk turtle. *Physiological Zoology* 22:172–178.
- ST. CLAIR, R. C., AND P. T. GREGORY. 1990. Factors affecting the northern range limit of Painted Turtles (*Chrysemys picta*): winter acidosis or freezing? *Copeia* 1990:1083–1089.
- TATTERSALL, G. J., AND R. G. BOUTILIER. 1997. Balancing hypoxia and hypothermia in cold-submerged frogs. *Journal of Experimental Biology* 200: 1031–1038.
- . 1999. Behavioural oxyregulation by cold-submerged frogs in heterogeneous oxygen environments. *Canadian Journal of Zoology* 77: 843–850.
- TAYLOR, G. M., AND E. NOL. 1989. Movements and hibernation sites of overwintering Painted Turtles in southern Ontario. *Canadian Journal of Zoology* 67:1877–1881.
- ULTSCH, G. R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. *Biological Reviews* 64: 435–516.
- . 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Reviews* 81:339–367.
- ULTSCH, G. R., AND D. C. JACKSON. 1982. Long-term submergence at 3°C of the turtle *Chrysemys picta bellii* in normoxic and severely hypoxic

- water—I. Survival, gas exchange, and acid-base status. *Journal of Experimental Biology* 96: 11–28.
- ULTSCH, G. R., M. E. CARWILE, C. E. CROCKER, AND D. C. JACKSON. 1999. The physiology of hibernation among Painted Turtles: the Eastern Painted Turtle *Chrysemys picta picta*. *Physiological and Biochemical Zoology* 72:493–501.
- ULTSCH, G. R., T. E. GRAHAM, AND C. E. CROCKER. 2000. An aggregation of overwintering Leopard Frogs, *Rana pipiens*, and Common Map Turtles, *Graptemys geographica*, in northern Vermont. *Canadian Field Naturalist* 114:314–315.
- WOOD, S. C., AND G. M. MALVIN. 1991. Physiological significance of behavioural hypothermia in hypoxic toads (*Bufo marinus*). *Journal of Experimental Biology* 159:203–21.

Accepted: 27 November 2007.