The physiology of hibernation in common map turtles

(Graptemys geographica)

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Received 30 April 2001; received in revised form 15 June 2001; accepted 26 June 2001

Abstract

Map turtles from Wisconsin were submerged at 3°C in normoxic and anoxic water to simulate extremes of potential respiratory microenvironments while hibernating under ice. In predive turtles, and in turtles submerged for up to 150 days, plasma PO2, PCO2, pH, [Cl−], [Na+], [K⁺], total Mg, total Ca, lactate, glucose, and osmolality were measured; hematocrit and body mass were determined, and plasma [HCO3⁻] was calculated. Turtles in anoxic water developed a severe metabolic acidosis, accumulating lactate from a predive value of 1.7 to 116 mmol/l at 50 days, associated with a fall in pH from 8.010 to 7.128. To buffer lactate increase, total calcium and magnesium rose from 3.5 and 2.0 to 25.7 and 7.6 mmol/l, respectively. Plasma [HCO3⁻] was titrated from 44.7 to 4.3 mmol/l in turtles in anoxic water. Turtles in normoxic water had only minor disturbances of their acid–base status and ionic statuses; there was a marked increase in hematocrit from 31.1 to 51.9%. This study and field studies suggest that map turtles have an obligatory requirement for a hibernaculum that provides well-oxygenated water (e.g. rivers and large lakes rather than small ponds and swamps) and that this requirement is a major factor in determining their microdistribution. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Common map turtles; Graptemys geographica; Hibernation; Acid–base balance; Ionic balance; Overwintering

1. Introduction

The ability to tolerate prolonged submergence by an air-breathing reptile or amphibian is a prerequisite for underwater hibernation. All northern species of freshwater turtles studied thus far can tolerate months of submergence in normoxic water at 3°C, although only painted turtles (Chrysemys picta) have been shown to tolerate months of submergence in anoxic water at that temperature (Jackson, 2000; Ultsch, 1989; Ultsch and Jackson, 1995). Studies to date suggest that there are two types of physiological responses to...
prolonged cold submergence among northern freshwater turtles that are in turn dependent upon whether hibernation (i.e. overwintering) occurs in well-oxygenated water (e.g. streams and rivers) or in hypoxic or anoxic hibernacula (e.g. swamps or mud, respectively). One response, typified by musk turtles (*Sternotherus odoratus*), is to become essentially an aquatic animal in terms of gas exchange in normoxic water (Ultsch, 1988; Ultsch and Cochran, 1994). Musk turtles accumulate relatively little lactate during 5 months of submergence at 3°C in normoxic water, have a slight decrease in plasma P<sub>CO</sub><sub>2</sub>, and maintain plasma pH; all indicating that they are essentially aerobic throughout the winter, utilizing extrapulmonary pathways for gas exchange. Softshell turtles (*Apalone spinifera*) react similarly to musk turtles when submerged in normoxic water (Jackson et al., 1984; Ultsch et al., 1984 and unpublished data). In contrast, neither of these species tolerates anoxic submergence well at 3°C, musk turtles surviving only approximately 3 weeks (Ultsch and Cochran, 1994) and softshells only approximately 2 weeks (Reese et al., unpublished data).

A second response is typified by painted turtles; they can tolerate long periods of cold anoxic submergence but cannot remain completely aerobic if the water is normoxic. Oxygenation of the water is beneficial to an overwintering painted turtle in that aquatic oxygen uptake enables a substantial reduction in the rate of development of an acidosis due to a much smaller, but still significant, lactate accumulation (Jackson et al., 2000; Reese et al., 2000; Ultsch and Jackson, 1982; Ultsch et al., 1999). Thus far, there appears to be an inverse relationship among turtle species in their ability to be aerobic when submerged in normoxic water and their ability to tolerate anoxic submergence.

The inability to tolerate a low ambient P<sub>O</sub><sub>2</sub> during overwintering appears to limit northern softshell and musk turtles to habitats that will provide hibernacula with well-oxygenated water (e.g. streams, rivers, and large lakes), while the ability to tolerate a low oxygen tension possibly explains why painted turtles are ubiquitous in all permanent bodies of water within their range. The ability to be aerobic while overwintering might seem to be due to an efficient cutaneous uptake of oxygen, as both musk and softshell turtles have a large amount of exposed and visibly vascularized skin, which is lacking in painted turtles. However, common map turtles (*Graptemys geographica*) are limited to the same sorts of habitats as softshell turtles, but they appear morphologically similar, and are closely related to, painted turtles. Furthermore, preliminary experimental data (Ultsch and Jackson, 1995) suggested that map turtle responses to simulated hibernation are much more like those of musk and softshell turtles than those of painted turtles, and a field study of naturally overwintering map turtles in a river in Vermont indicated that the turtles were almost entirely aerobic throughout the winter in their well-oxygenated hibernaculum (Crocker et al., 2000).

Here we report on studies of simulated hibernation in common map turtles from Wisconsin and show that they are entirely aerobic when submerged in normoxic water at 3°C, but fare poorly during anoxic submergence, a lethal acidosis being attained in approximately 50 days. We conclude that an inability to tolerate prolonged anoxia, and likely significant hypoxia, excludes map turtles from aquatic habitats that are subject to a substantial wintertime oxygen decrement.

2. Materials and methods

2.1. Animals

Common map turtles (*Graptemys geographica*) were collected during the summers of 1997–1999 in La Crosse County, Wisconsin under permit from the Wisconsin Department of Natural Resources. All turtles were collected, housed and fed similarly and used in the winter following their collection. Turtles were housed in an AAALAC (Association for Assessment and Accreditation of Laboratory Animal Care International)-approved aquatic facility at the University of Alabama at approximately 20°C, using well water neutralized with marble chips. They were fed catfish food pellets supplemented with whole fish. Basking platforms were illuminated with plant lights on a 12D–12L photoperiod.

2.2. Blood sampling and analyses

The methodologies for simulating hibernation and for sampling blood were similar to those of Ultsch et al. (1999). Briefly, in early October, we ceased feeding the turtles and then moved them...
into a cold room at 15°C 3 days later. They were split into two groups and placed in shallow water (10 cm), where they were cooled at 1°C/day to 3°C, at which they were maintained for 3 days. Control (predive) blood samples were taken from five turtles over each of two study cycles. Samples were taken by cardiac puncture following decapitation and pithing. Access to the heart was gained via a 2-cm hole trephined in the plastron. A heparinized (100 000 units/l ammonium heparin in turtle ringer’s solution) glass syringe was used to withdraw an anaerobic aliquot of blood (approx. 0.4–0.6 ml), which was immediately analyzed for pH, Po2, and Pco2 in a Radiometer BMS 3 MK2 Blood Micro System and PHM 73 pH/blood-gas monitor thermostatted at 3°C. The CO2 electrode output was read as pH (Radiometer PHM 240 pH/ion meter) and converted to Pco2 using the linear relationship between log Pco2 and pH. Blood-gas electrodes were calibrated with gas mixtures supplied from a Wösthoff M301/a-F gas-mixing pump; the pH electrode was calibrated with precision buffers (Radiometer).

The turtle was then placed plastron upward on an elevated stand, and a 20-gauge needle with attached catheter (PE-90) tubing was inserted into the ventricle; blood pumped by the heart into the catheter was collected into microcentrifuge tubes as it drained. The tubes were centrifuged (3 min at 10 000 g) and the decanted plasma was stored at −80°C. Two microhematocrit tubes were filled from the catheter and hematocrit was determined by centrifugation for 4 min at 13 000 × g. The stored plasma was later used for analysis of [Na+] and [K+] (Radiometer FLM 3 flame photometer), [Cl−] (Radiometer CMT10 chloride titrator), lactate and glucose (YSI 2300 Stat-Plus Analyzer), total Mg and Ca (Perkin-Elmer 280 atomic absorption spectrophotometer; therefore, measurements included all forms of these elements, not just the free cations), and osmolality (Precision Systems \( \mu \text{Osmette} 5004 \)). Plasma \( \text{HCO}_3^- \) was calculated using the Henderson–Hasselbalch equation (\( \alpha_{\text{CO}_2} = 0.0812 \), Reeves 1976) and a pK’ that depended on the blood pH (Jackson and Heisler, 1983): 6.293 for control turtles and submerged turtles with a pH ≥ 7.932 (the lowest pH of a control turtle) and 6.350 for turtles with a pH < 7.932.

Each group of remaining turtles was maintained submerged by placing a plastic grate approximately halfway down into the water column above them. The water in one tank was maintained normoxic (approx. 158 mmHg) by aerators that drew air from outside the cold room. A second identical tank was covered with a plastic lid and nitrogen was bubbled through airstones above the grate, which maintained the water Po2 at < 5 mmHg, usually 0–2 mmHg. The water in both tanks was flushed occasionally with pre-equilibrated water at 3°C, without allowing the turtles to breathe. Viability was determined periodically by vigorous prodding of the head and extremities to elicit movements. A failure to respond was considered evidence of death. Even though some unresponsive turtles were found to have a weak heartbeat upon removal, turtles in such a condition did not recover upon air access and warming and can be considered ecologically dead; thus we consider a failure to respond to be a reasonable viability endpoint, as has been found to be the case in previous studies (Ultsch, 1988; Ultsch et al., 1999).

Submerged turtles were removed for blood sampling as described above, except that they were prevented from breathing by clamping the neck. A 12D–12L photoperiod of muted light was maintained throughout the experiment. Sampling was scheduled for both groups on days 0 (predive controls), 5, 15, 25, 50, 75, 104, 125 and 150; however, no anoxic turtles survived the 50–75-day interval.

2.3. Statistics

Statistical analyses were performed with Statistica at the 0.05 level of significance. Comparisons were done with MANOVA, one-way ANOVA, and a Kruskal–Wallis test when appropriate. Student–Newman–Keuls, Bonferonni, or Tukey’s HSD tests were used for multiple comparisons. Data are given as mean ± S.E. Data from a single turtle sampled after 219 days of submergence in normoxic water were excluded from statistical analyses.

3. Results

3.1. Viability and mass gain

Two of the seven turtles in anoxia until day 50 were dead, one was flaccid but did have a heart-
beat and could be sampled, and four were weakly responsive and with a very low blood pH that suggested they were near death. These observations and previous data (Ultsch and Jackson, 1995) suggest that the limit of anoxia tolerance of map turtles under these conditions is approximately 50 days. In contrast, two of five turtles submerged in normoxic water in a separate experiment recovered after 180 days, and two more recovered after 217 days, when allowed access to air, warmed to room temperature overnight, and placed in a tank with shallow water and a basking platform. The fifth turtle was removed, while still quite responsive, for blood sampling after 219 days of submergence. For the two turtles still alive in normoxic water after 180 days, mass increased in a 56.3-g turtle by 3.73% (0.021%/day) and in a 48.2-g turtle by 3.94% (0.022%/day). All turtles gained mass, although rates varied considerably; mass gain among turtles in normoxic water occurred at a lesser rate than among those in anoxic water (Table 1).

3.2. Extrapulmonary gas exchange

We assumed that the \( P_O_2 \) of turtles submerged in anoxic water was zero and that any greater measured value was due to sample contamination; these turtles are hereafter referred to as anoxic turtles. We used the mean measured difference from zero in samples from anoxic turtles to correct the \( P_O_2 \) data for turtles sampled from normoxic water the same day. The mean correction ranged from 0.3 to 0.8 mmHg. The \( P_O_2 \) of turtles in normoxic water was always very low, from 0.5 to 0.6 mmHg through day 25 and from 1.1 to 2.0 mmHg from day 50 to 150. The \( P_CO_2 \) of anoxic turtles tended to fall, although not significantly, throughout 50 days of submergence, while the \( P_CO_2 \) of turtles in normoxic water did fall significantly during the first 25 days of submergence to 5.32 ± 0.23 mmHg, from an initial level of 10.74 ± 0.44 mmHg, and then remained stable through day 150 (Fig. 1a).

3.3. Acid–base and ionic statuses

Blood pH of anoxic turtles fell rapidly and steadily, reaching 7.128 ± 0.057 at day 50. The pH of turtles in normoxic water remained unchanged after 150 days of submergence (Fig. 1b). The plasma \( [HCO_3^-] \) in anoxic turtles fell to low levels (4.32 ± 0.68 mmol) after 50 days, but never below 10% of control values; \( [HCO_3^-] \) in turtles in normoxic water remained unchanged after 150 days of submergence (Fig. 1b). The plasma \( [HCO_3^-] \) fell to low levels (4.32 ± 0.68 mmol) after 50 days, but never below 10% of control values; \( [HCO_3^-] \) in turtles in normoxic water remained unchanged after 150 days of submergence (Fig. 1b).

| Table 1 |
| Predive values for body mass, blood gasses, acid–base variables, Hct, ions, total Ca and Mg, osmolality, and glucose compared to the values for the same variables after 50 days of submergence of Garaptemys geographica in normoxic and in anoxic water, and after 150 days of submergence in normoxic water, all at 3°C |

<table>
<thead>
<tr>
<th></th>
<th>Predive (n = 10)</th>
<th>Normoxic water (50 days)</th>
<th>Anoxic water (50 days)</th>
<th>Normoxic water (150 days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight gain (%)</td>
<td>–</td>
<td>3.00 ± 1.61 (4)(^{a,b})</td>
<td>5.82 ± 0.91 (4)(^{a})</td>
<td>6.80 ± 1.57 (3)(^{a})</td>
</tr>
<tr>
<td>( P_O_2 ) (mmHg)</td>
<td>40.7 ± 6.5</td>
<td>1.4 ± 0.30(^{a,b})</td>
<td>0.9 ± 0.76(^{a})</td>
<td>1.2 ± 0.2(^{a,b})</td>
</tr>
<tr>
<td>( P_CO_2 ) (mmHg)</td>
<td>10.74 ± 0.44</td>
<td>5.77 ± 0.34(^{a})</td>
<td>8.50 ± 0.76(^{a})</td>
<td>5.63 ± 0.36(^{a})</td>
</tr>
<tr>
<td>pH</td>
<td>8.010 ± 0.029 (5)</td>
<td>8.116 ± 0.009(^{b})</td>
<td>7.128 ± 0.057(^{a})</td>
<td>8.052 ± 0.020(^{b})</td>
</tr>
<tr>
<td>([HCO_3^-]) (mmol/l)</td>
<td>44.68 ± 1.93 (5)</td>
<td>31.20 ± 1.98(^{b})</td>
<td>4.32 ± 0.68(^{b})</td>
<td>26.12 ± 0.83(^{b})</td>
</tr>
<tr>
<td>([Na^+]) (mmol/l)</td>
<td>123.2 ± 2.7 (5)</td>
<td>118.0 ± 2.2</td>
<td>112.7 ± 2.6</td>
<td>111.9 ± 2.0</td>
</tr>
<tr>
<td>([K^+]) (mmol/l)</td>
<td>2.36 ± 0.14</td>
<td>2.03 ± 0.22(^{b})</td>
<td>7.87 ± 0.71(^{b})</td>
<td>1.90 ± 0.52(^{b})</td>
</tr>
<tr>
<td>([Cl^-]) (mmol/l)</td>
<td>86.0 ± 1.2</td>
<td>86.6 ± 3.3(^{b})</td>
<td>66.1 ± 2.4(^{b})</td>
<td>80.9 ± 1.6(^{b})</td>
</tr>
<tr>
<td>Total Mg (mmol/l)</td>
<td>2.03 ± 0.13</td>
<td>1.18 ± 0.08(^{a,b})</td>
<td>7.58 ± 0.79(^{b})</td>
<td>1.54 ± 0.11(^{b})</td>
</tr>
<tr>
<td>Total Ca (mmol/l)</td>
<td>3.53 ± 0.27</td>
<td>1.56 ± 0.13(^{a,b})</td>
<td>25.7 ± 3.90(^{a})</td>
<td>2.28 ± 0.34(^{a})</td>
</tr>
<tr>
<td>Lactate (mmol/l)</td>
<td>1.66 ± 0.19</td>
<td>2.48 ± 0.16(^{a})</td>
<td>116.0 ± 5.2(^{a})</td>
<td>2.4 ± 0.45(^{a})</td>
</tr>
<tr>
<td>Glucose (mmol/l)</td>
<td>1.72 ± 0.20</td>
<td>1.08 ± 0.19(^{b})</td>
<td>9.48 ± 4.48</td>
<td>1.74 ± 0.16(^{b})</td>
</tr>
<tr>
<td>Osmolality (mOsm/kg plasma)</td>
<td>249 ± 4</td>
<td>232.2 ± 5(^{b})</td>
<td>330 ± 13(^{a})</td>
<td>217 ± 5(^{b})</td>
</tr>
</tbody>
</table>

Note: Values are means ± S.E. Numbers in parentheses are sample sizes when different from column values.

\(^{a}\)Significantly different from predive values (ANOVA).

\(^{b}\)Significantly different from 50-day anoxic values (ANOVA).
moxic water also fell, but final values never dropped below 58% of predive values (Fig. 1c). A pH–[HCO₃⁻] (Davenport) diagram (Fig. 2) indicates that there was a mild respiratory alkalosis combined with a severe metabolic acidosis in anoxic turtles, while there was a slight respiratory alkalosis among turtles in normoxic water with no metabolic acidosis.

Time-course changes in plasma ions and lactate are given in Fig. 3a–f. Mean predive and final (50 days submergence in anoxic water and 150 days in normoxic water) data are given in Table 1, along with data for 50 days of submergence in normoxic water for comparison to final (50 day) data for anoxic turtles. Except for Na⁺, all measured plasma ion concentrations changed significantly in anoxic turtles; total Ca, total Mg, and K⁺ increased, and Cl⁻ decreased. Except for a decrease in total Ca, no significant ionic changes were observed in turtles in normoxic water. Lactate concentrations also changed in anoxic turtles only, where they rose dramatically.

3.4. Hematocrit, glucose, and osmolality

Hematocrit tended to increase with time of submergence, but the change was not significant by the time either group had been submerged 50 days; it was significantly elevated in turtles in normoxic water (as high as 66% in one animal) after 150 days (Fig. 4a). Osmolality increased 32.4% after 50 days of submergence in anoxic turtles, largely due to lactate accumulation, while decreasing 12.6% in turtles submerged in normoxic water for 150 days, presumably due to water uptake (Fig. 4b). Increases in glucose concentration were sporadic, and mainly limited to anoxic turtles that were near death, in which case they often spiked to as high as 24 mmol/l (Fig. 4c).

4. Discussion

4.1. Submergence in normoxic water

The only remarkable physiological response of *Graptemys geographica* to simulated hibernation in normoxic water during 5 months of submergence is a non-lethal water uptake as evidenced by the weight gain measured in the turtles. In spite of a very low blood \( P_{O_2} \) (approx. 0.5–2.0 mmHg), the turtles are clearly entirely aerobic, as indicated by the lack of even a slight lactate accumulation. Metabolic depression is undoubtedly an important component of this ability, but the animals are nevertheless not entirely torpid. They respond to touch and can withdraw head and limbs quickly. Field observations of naturally hibernating *G. geographica* in Vermont confirm both the low blood \( P_{O_2} \) (Crocker et al., 2000) and the relative alertness and ability to move during natural hibernation (Ultsch et al., 2000; Crocker, 2001).
Fig. 2. Changes in acid–base status of turtles submerged in normoxic (open circles) or anoxic (filled circles) water at 3°C, as depicted by a pH–[HCO₃⁻] (Davenport) diagram. The duration of submergence is indicated next to each sample mean.

Personal observations while scuba-diving at a map turtle hibernaculum). Thus, the ability to utilize extrapulmonary oxygen uptake is sufficient to supply not only resting metabolic rates, but also to maintain either a small aerobic scope for activity, or enough O₂ transport capacity to repay any oxygen debt associated with an anaerobic burst of activity. Additional factors permitting a sufficient O₂ uptake and transport are likely to include an extreme left-shift of the O₂ dissociation curve (Maginniss et al., 1983) and an increased red blood cell count (Saunders et al., 2000); this later effect can be seen as an increase in hematocrit in the map turtles (Table 1).

Extrapulmonary gas exchange was also sufficient for eliminating CO₂, not only for turtles in normoxic water, but also for those in anoxic water. A metabolic depression of turtles in normoxic water would lower the rate of CO₂ production, here apparently so much so that even without the
pulmonary elimination of CO₂, PₐCO₂ fell substantially. The efficacy of cutaneous, and possibly buccopharyngeal, elimination of CO₂ is especially apparent in that turtles in anoxic water did not develop a transient respiratory acidosis due to acid-titration of blood bicarbonate, as is typically the case in painted turtles (Ultsch and Jackson, 1982; Ultsch et al., 1999). Such titration undoubtedly occurred, but the resultant CO₂ was eliminated so rapidly that there was no significant increase in plasma PₐCO₂.

After 5 months of submergence in normoxic water, there were no physiologically important changes in either acid–base status (Fig. 2), or ionic charge distribution (summarized as a plasma ion balance diagram, ‘Gamblegram’ in Fig. 5). A clue concerning the ultimate limiting factor for survival during submergence does appear, however, at day 150 in the form of a significant drop in osmolality, which suggests the beginning of a failure of water balance regulation. Moreover, one turtle submersed for 219 days had a pH of 7.970, a [HCO₃⁻] of 22.33, a PₐCO₂ of 5.79, and a PₐO₂ of 0.8 mmHg, all of which are similar to corresponding values for turtles submersed for 150 days, in spite of a [lactate] of 20 mmol/l. The measurements on this turtle, plus the recovery of others kept submersed in normoxic water for a similar period, suggests that gas exchange with the water and acid–base balance is not severely compromised, even after periods that exceed those expected to be encountered in the field. However, this turtle had a [Cl⁻] of 48 mmol/l, a [Na⁺] of 85.0 mmol/l, and an osmolality of 173 mOsm/kg plasma, all of which are well below the corresponding values for turtles submersed for 150

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**Fig. 4.** As in Fig. 1, for hematocrit, osmolality, and glucose.

**Fig. 5.** Plasma anion and cation concentrations, as depicted by a ‘Gamblegram’ to show charge balance, for turtles submersed in normoxic and anoxic water.
days and strongly suggest a dilution of the plasma, and likely of other body fluid compartments, by water influx.

### 4.2. Submergence in anoxic water

The responses of *G. geographica* submerged in anoxic water qualitatively resemble those of other species under similar conditions (Ultsch and Cochran, 1994; Jackson et al., 1984; Ultsch, 1989); these responses are ultimately all related to the rapid and profound increase in lactate generated by anaerobiosis. The protons associated with lactate formation titrated [HCO$_3^-$] to 10% of its pre-dive values by day 50, but the fact there was still measurable bicarbonate, along with the fact that the initial bicarbonate should have all been titrated by day 15, indicates that bicarbonate was being replaced from elsewhere, the likely source being the skeleton, in particular the shell, and the accompanying cations being mainly calcium and magnesium (Fig. 5) (Jackson, 2000; Jackson et al., 2000).

Although the turtles developed a severe lactacidosis, they were able to survive approximately 50 days. Two mechanisms prevented an earlier death. The first was the lack of a respiratory component to the acidosis; in fact there was a trend in the anoxic turtles toward a compensatory respiratory alkalosis in spite of the lack of ventilatory regulation of $P_{CO_2}$. More importantly, the decrease in the SID (strong ion difference) was attenuated from what would have occurred if the increase in [lactate] was not ionically compensated. Stewart (1981) has argued that plasma pH is a dependent variable whose value is determined by three independent variables — $P_{CO_2}$, SID, and the sum of weak acids, with the first two being the variables that are primary regulators. As mentioned, without the possibility of hyperventilation, $P_{CO_2}$ in the submerged turtles will be set largely by a balance of metabolic rate and passive diffusion processes, perhaps enhanced by cutaneous vasodilation. For the turtles, the main compensatory mechanism is regulation of the SID, where lactate must be considered as a strong ion. With no changes in ions other than lactate, SID would quickly become negative and fall as low as $-70$ mEq/l by 50 days of anoxic submergence, with an associated lethal pH (Fig. 6). The potential fall in SID can be minimized by increases in the concentrations of strong cations or decreases in the concentrations of strong anions, and both occur. The only ion that changes in the ‘wrong’ direction is Na$^+$, which decreased after 50 days by approximately $10$ mEq/l; [K$^+$], total Ca, and total Mg all increased, while [Cl$^-$] decreased, all of which contributed to the SID being reduced by 50 days to $-0.5$ mEq/l, rather than the potential $-70$ mEq/l, a 62% compensation. In addition to the ionic changes, considerable lactate is likely sequestered in the shell, further defending the extracellular pH (Jackson, 2000).

### 4.3. Comparative and ecological considerations

Map turtles are closely related to painted turtles (both family Emydidae) and distantly related to musk (family Kinosternidae) and softshell turtles (family Trionychidae). However, in terms of survival when submerged in anoxic water, and an ability to be completely aerobic when submerged in normoxic water, map turtles resemble musk and softshell turtles more than painted turtles. Considering the demonstrated importance of the shell in tolerating anoxic submergence (Jackson, 1999), the inability of map turtles to tolerate anoxia as well as painted turtles from the same area is surprising, as map turtles possess an extensive shell. A comparison of parameters after 50 days of anoxic submergence appears to supply a likely explanation (Table 2). The key is the 32%
Map turtles provide another example (in addition to musk and softshell turtles) of the correlation of a relatively poor ability to tolerate anoxia with a well-developed ability to function as essentially an aquatic animal while hibernating in normoxic water. The ecological result is that such species appear to be limited to habitats that will reliably provide a hibernaculum in which the water is well-oxygenated. Thus, map and softshell turtles, particularly in the northern portions of their ranges, are typically riverine species or found in large lakes, habitats that will not become hypoxic or anoxic during the portion of the winter when they are ice-covered. To inhabit other areas, such as swamps and small, shallow ponds, in which painted turtles are common, would require migrating to a suitable hibernaculum, a strategy that does not appear to be used. In this regard, musk turtles are particularly interesting. While softshell and map turtles are primarily found in the same types of habitats in the southern portion of their range as in the northern, common musk turtles in the south also inhabit swamps and shallow ponds, habitats that they appear to avoid near their northern limits.

How other species of northern turtles cope with potential anoxia remains an open question. Snapping turtles (Chelydra serpentina) range as far north as painted turtles, and like them, are also found in virtually all bodies of permanent water. Therefore, it seems likely that they are also more tolerant of anoxia than map and softshell turtles, and we have preliminary data on Chelydra from Michigan that shows that snapping turtles survive anoxic submergence at 3°C more than twice as long as map turtles, and four and nine times as long as musk and softshell turtles, respectively. Physiological data on other northern species are lacking.

Acknowledgements

We thank Sharmilee Bansal, Marcus Jones, Cheré LeBerte, Bradley Marker, Walter Smith, and E. Ray Stewart for their aid in various aspects of this study. We also thank Neal Paisley and the Wisconsin Department of Natural Resources for their help in obtaining the turtles. This research was supported by National Science Foundation grants IBN-96-03934 (to GRU) and

Table 2
A comparison of plasma variables of common map turtles (Graptemys geographica) and western painted turtles (Chrysemys picta bellii), both from Wisconsin, after 50 days of submergence in anoxic water at 3°C

<table>
<thead>
<tr>
<th></th>
<th>Map turtles</th>
<th>Western painted turtles</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Control 50 days anoxic</td>
<td>Control 50 days anoxic</td>
</tr>
<tr>
<td>pH</td>
<td>8.010</td>
<td>8.060</td>
</tr>
<tr>
<td>HCO₃⁻ (mmol/L)</td>
<td>44.68</td>
<td>46.42</td>
</tr>
<tr>
<td>PCO₂ (mmHg)</td>
<td>10.74</td>
<td>9.90</td>
</tr>
<tr>
<td>Lactate (mmol/L)</td>
<td>1.66</td>
<td>1.6</td>
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<tr>
<td>Na⁺ (mmol/L)</td>
<td>123.2</td>
<td>131.0</td>
</tr>
<tr>
<td>K⁺ (mmol/L)</td>
<td>2.36</td>
<td>2.14</td>
</tr>
<tr>
<td>Cl⁻ (mmol/L)</td>
<td>86.0</td>
<td>84.0</td>
</tr>
<tr>
<td>Mg (mmol/L)</td>
<td>2.03</td>
<td>2.7</td>
</tr>
<tr>
<td>Ca (mmol/L)</td>
<td>3.53</td>
<td>3.2</td>
</tr>
<tr>
<td>Osmolality (mOsm/kg plasma)</td>
<td>249</td>
<td>277</td>
</tr>
<tr>
<td>SID (mEq/l)</td>
<td>43.4</td>
<td>−0.5</td>
</tr>
</tbody>
</table>
| Data for C. p. bellii for 50 days of anoxic submergence are from Jackson et al. (2000), except for pH, which is an average of 25 and 75-day values. Lower rate of lactate accumulation in the western painted turtles, which suggests that they are able to depress metabolic rate more than map turtles when anoxic. The lower rate of anaerobic lactate production causes a lesser depression of pH, associated with a much smaller decrease in the SID. Perhaps because other regulatory systems are functioning better in painted turtles, they do not have the water influx seen in map turtles as an increase in osmolality. Both species will die when plasma pH falls to approximately 7.0–7.1 (as is the case for all species studied under these conditions); however, painted turtles are able to forestall this fatal fall in pH by their presumed lower metabolic rate.

Why map turtles can remain aerobic while submerged during hibernation while painted turtles accumulate significant amounts of lactate is an open question. Two possibilities are that map turtles lower their metabolic rate during hibernation more than painted turtles, or that map turtles have more efficacious mechanisms for extrapulmonary oxygen uptake. The lower rate of lactate accumulation of painted turtles in anoxic water mentioned above does not support the former hypothesis, which suggests that the map turtles are better able to utilize dissolved oxygen. However, this conclusion remains tentative.
IBN-97-28794 (to DCJ) and a grant from the Northern Prairie Wildlife Research Center of the United States Geological Survey (to GRU). Animal use was under the guidelines and approval of the University of Alabama Animal Care and Use Committee.

References


