Effects of humidity, temperature, and submergence behavior on survivorship and energy use in hibernating garter snakes, Thamnophis sirtalis

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Desiccation is likely an important factor influencing winter mortality rates of terrestrial hibernating reptiles; however, this notion has not been rigorously tested. Groups of eastern garter snakes (Thamnophis sirtalis sirtalis) were matched for size and subsequently exposed to simulated hibernative conditions (5 or 12°C, under different humidity regimes) during winter, for 165 days or until all group members expired. As garter snakes in some dens submerge during natural hibernation, an additional group was maintained in water at 5°C. Snakes kept in air dehydrated and died (body water contents at death ranged from 62.1 to 67.8% of lean fresh mass), whereas snakes kept in water remained hydrated (median, 75.2%) and survived. Survival duration of air hibernators was inversely related to rate of mass loss, which in turn was strongly influenced by ambient humidity and temperature. Dehydration accounted for most of the mass lost in all air hibernators; however, owing to higher rates of nutrient consumption, mass loss was significantly greater in snakes kept at 12°C (36%) than in snakes kept at 5°C (29%). Changes in fat body and liver masses showed that snakes kept in air at 12°C used the most energy whereas those kept in water at 5°C used the least. Submerged hibernation behavior has significant survival value because under these conditions snakes remain hydrated during winter. Also, because submerged snakes conserve more stored energy during winter, their reproductive success may be enhanced when mating activities resume in early spring.


La dessiccation est probablement un important facteur de mortalité hivernale chez les reptiles qui font leur hibernation sous terre; cependant, cette proposition n’a jamais fait l’objet de tests rigoureux. Des Couleuvres rayées (Thamnophis sirtalis sirtalis) ont été regroupées selon leur taille et exposées par la suite à des conditions d’hibernation simulées (5 ou 12°C, à divers régimes d’humidity) au cours de l’hiver, durant 165 jours ou jusqu’à l’expiration de tous les membres du groupe. Il arrive parfois que des couleuvres soient submergées dans leur terrier durant l’hibernation en nature; un groupe supplémentaire de couleuvres a été gardé dans l’eau à 5°C. Les couleuvres gardées à l’air se sont déshydratées et sont mortes (le contenu hydrique total à la mort variait de 62.1 à 67.8% de la masse totale sans les graisses), alors que les couleuvres gardées dans l’eau sont restées humides (médiane, 75.2%) et sont survécues. La durée de la survie des couleuvres à hibernation aérienne était en relation inverse avec le taux de perte de masse, lui-même fortement influencé par l’humidity et la température ambiantes. La déshydratation était le principal facteur de perte de masse chez toutes les couleuvres à hibernation aérienne; cependant, à cause des taux plus élevés de consommation d’éléments nutritifs, la perte de masse était significativement plus grande chez les couleuvres gardées à 12°C (36%) que chez les couleuvres gardées à 5°C (29%). Les changements de masse du corps gras et du foie indiquent que ce sont les couleuvres gardées à l’air à 12°C qui ont utilisé le plus d’énergie et les couleuvres gardées dans l’eau à 5°C qui en ont utilisé le moins. Le comportement d’hibernation dans l’eau a donc une importante valeur de survie puisqu’il permet aux couleuvres de rester hydratées durant l’hiver. De plus, comme les couleuvres submergées conservent une plus grande partie de leur énergie durant l’hiver, leur succès à la reproduction est probablement plus grand au printemps.

Introduction

Snakes inhabiting high latitudes are routinely confronted with long cold winters and consequently may spend more than half of their annual time budget in hibernation (Gregory 1982; Costanzo 1988). As snakes do not feed during hibernation, they must rely entirely upon stored nutrients to meet metabolic demands during winter. Gregory (1982) suggested that the principal mortality factor in hibernating reptiles is exposure to lethal temperatures, yet some studies have implied that starvation during winter may be a contributing factor (e.g., Aleksiuk and Stewart 1971; Bauwens 1981).

High mortality rates have occasionally been reported for overwintering snake populations (e.g., 34–50% in three species (Hirth 1966); 18–47% in Vipera berus (Vittanen 1967); 35–50% in Thamnophis sirtalis (Gregory 1977)), and the loss of substantial amounts of body mass (e.g., up to 18% in adult Crotalus viridis (Parker and Brown 1974); up to ca. 25% in C. viridis hatchlings (Hirth 1966; Chairland 1987)) during hibernation has probably reinforced the common belief that nutrients are severely depleted during the extensive period of winter aphagia. Conversely, winter mortality in other den populations is reportedly slight (e.g., Parker and Brown 1974; Gregory 1982; Costanzo 1986; Larsen and Gregory 1989); snakes often contain large amounts of storage lipid (chiefly abdominal fat bodies) and are in good physiological condition at the time of spring emergence (e.g., Brown et al. 1974; Parker and Brown 1980; Costanzo 1985). This dichotomy may be partly due to varied metabolic demands imposed by the differential thermal microenvironments occupied by snakes during hibernation, but this suggestion has not been tested directly (Gregory 1982).

Cutaneous water loss in squamates is effectively inhibited by epidermal lips (Roberts and Lillywhite 1980; Graves et al. 1986). Behavioral modifications, such as aggregation, also function to conserve body water (Noble and Clausen 1936; Graves et al. 1986). Desiccation may nevertheless be an additional (and perhaps more important) cause of winter mortality because even in humid air, reptiles can lose a substantial amount of water over the long winter period. The effect of dehydration on the survivorship of overwintering snakes has not been adequately studied.

Traduit par la revue
In nature, hibernating snakes occupy den microsites that vary widely in ambient humidity regimes. Although many snakes use dry hibernacula, several colubrid and viperid species (see Table 7.5, Costanzo 1988) reportedly overwinter partially or completely submerged in standing water within dens. These snakes probably remain in water balance without difficulty, hence, mortality due to desiccation should be non-existent. Also, as a result of reduced behavioral activity and limited oxygen availability, completely submerged garter snakes apparently expend less energy during winter than do those hibernating in air (Costanzo 1989).

This investigation evaluated the following hypotheses: (i) high rates of moisture loss in hibernating snakes correspond to high winter mortality rates; (ii) behavioral aggregation, for the purpose of reducing rates of moisture loss, is more prominent among snakes exposed to drier air during hibernation; and (iii) energy consumption during hibernation is greater at higher body temperatures, and at similar temperatures, submerged snakes expend less energy than those hibernating in air.

Materials and methods

Eastern garter snakes (Thamnophis sirtalis sirtalis) were collected by hand during early October as they approached a communal hibernaculum in central Wisconsin. Previous study suggested that these snakes would soon commence hibernation (Costanzo 1986). In the laboratory, snakes were weighed to 0.1 g and assigned to six treatment groups (N = 8 each); snakes were matched for size so that sample means and variances for body mass did not differ statistically (ANOVA, F = 0.21; Bartlett’s test for homoscedasticity, 8.2) among groups. Four of the groups, used for determination of energy use, consisted of males only; the remaining groups were composed of snakes of both sexes.

The snakes in one all-male group (hereafter referred to as the initial group) were immediately sacrificed and assayed for prehibernation lean body water content and isolated fat body mass. Two all-male and two mixed-sex groups were housed in special cages (26 cm long x 24 cm wide x 18 cm high) constructed from a wooden frame with a wire screen floor and front and clear polyethylene walls. The front had a door that allowed access to the snakes; an overlying flap of plastic was used to seal the cage when access was not desired. Humidity inside the cages was maintained at desired levels by placing the cages directly over enameled pans containing deionized water or saturated solutions of CaCl₂ or NaCl. Cage humidity was measured periodically over the course of the study by means of a hygrometer (Hytrogenst, model 6250, Testoterm Inc., Mount Freedom, NJ).1 A separate all-male group was housed in a clear plastic tub filled with deionized water reconstituted to 79 mg/L (the hardness of water in the Wisconsin den (Costanzo 1989), to within 2 cm of a wire-screen top. A partly flattened loop of large-mesh wire screen, fastened to a rock and submerged in the tub, allowed snakes to anchor themselves underwater. All cages were kept in darkened environmental chambers at 5 or 12°C.

Snakes were kept in the cages for 165 d, the typical period of natural hibernation in the Wisconsin den (Costanzo 1986, 1988), or until they died. The number of air-hibernating snakes located within each quadrant of the cage floor was recorded at ca. 10-d intervals; sampling of the snakes’ positions continued, for each cage, until the first member of the group died. After their positions were recorded, snakes were removed from the cages, weighed quickly to 0.1 g, and then replaced. Those hibernating in water (submerged group) were carefully blotted until a constant measurement was obtained. All snakes were visually examined for mortality, under indirect low-level illumination, at 1- to 2-d intervals. Following discovery of the first death, however, snakes were checked more frequently (usually morning and evening).

Fat bodies and livers of dead snakes were quickly excised and weighed to 0.001 g. To determine moisture contents, livers and the remainder of lean carcasses were dried separately at 40°C to constant mass. Total lean body water content was calculated by combining values for liver and carcass. Snakes that survived for 165 d were sacrificed and processed similarly.

Mass changes of snakes during hibernation were determined by comparing the mass of individuals at the time of their death with that measured just before experimentation. Rates of mass loss were determined from successive mass measurements made during routine sampling. The resulting series of rates (first and last values excluded) was then averaged to produce a value for each individual.

Energy use during hibernation was inferred from differences in fat body and dry liver masses among all-male treatment groups. This sex restriction was necessary because the high variability in fat body masses of females (Costanzo 1985; P. Costanzo, unpublished data) would have obscured changes. Changes in lipid content were calculated from the difference of each animal’s mean fat body mass at the start of the experiment and that determined for each all-male treatment group. Rates of lipid utilization, incorporating each group’s median survival time, were based upon the resulting estimates of the quantity of lipid utilized.

Differences in final masses and moisture contents of carcasses and body components among treatment groups were assessed using Kruskal–Wallis tests; Dunn’s separation test was employed whenever significant differences occurred. Median body water content of snakes in the submerged group was compared with that of the initial group by means of the Mann–Whitney U-test for independent samples. This test was also used to compare rates of mass loss, final hydration states, and the proportion of initial mass lost by the time of death between male and female snakes. Median body masses of submerged snakes, determined before and after hibernation, were compared using the Wilcoxon matched-pairs signed-ranks test. All nonparametric statistical procedures followed Siegel (1956); significance was judged, a priori, at P < 0.05.

Results

Mean ± 1 SEM vapor pressure deficits (VPD) inside the three cages kept at 5°C were 0.16 ± 0.01 kPa (85% RH), 0.27 ± 0.01 kPa (75% RH), and 0.39 ± 0.01 kPa (55% RH). The mean VPD inside the cage kept at 12°C was 0.21 ± 0.02 kPa (85% RH). Humidity regimes inside all cages remained fairly stable over the course of the study. One snake from the 0.39 kPa group escaped from the cage soon after the start of the experiment; however, the recalculated mean for initial body mass (34.2 g, N = 7) was not appreciably different from that determined originally (32.8 g, N = 8).

Survival duration of air hibernators, based on sample medians and lethal times (LT₅₀) calculated using probit analyses, generally increased with increasing cage humidity. Of the 31 snakes kept in air, only 2 (from the group exposed to the lowest VPD regime) survived for 165 d. In contrast, all eight submerged hibernators survived this period (Table 1).

Rates of mass loss in air hibernators differed significantly (P = 0.001) among all treatment groups. Snakes kept at higher humidity regimes generally had lower rates of mass loss, but intragroup rates of mass loss were variable and many values overlapped those of individuals in other treatment groups (Fig. 1). Survival durations of snakes in all air-hibernating groups were inversely related to individual rates of

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1Because saturation vapor pressure varies with temperature, it is inappropriate to use relative humidity as a measure of the drying power of a gas only if sample temperatures are uniform. Values for vapor pressure deficit, a thermally independent equivalent, are reported in the present study.
mass loss, although snakes kept at 12°C lost mass more rapidly relative to those with comparable survivorship durations kept at 5°C (Fig. 1). The proportion of prehibernation mass lost by the time of death did not differ among the three groups of air hibernators kept at 5°C. However, median values for these groups were higher (P < 0.001) than those for snakes kept at 12°C (Table 2).

The median mass of submerged snakes changed little (from 28.6 to 27.6 g) by 165 d of hibernation; however, changes calculated for individual snakes actually ranged from +5 to −8% of prehibernation mass (Fig. 2). Mass change in these snakes was directly related (P = 0.05) to changes in water content.

Lean body water contents of air hibernators, measured at the time of their death, did not differ (P = 0.312) among treatment groups; pooled values ranged from 62.1 to 67.8% of fresh mass (median, 64.9%). Corresponding liver moisture contents also did not differ (P = 0.185) among all air hibernators, but these values were generally higher (63.2–71.5%; median, 67.6%) and more variable than lean body water contents (Fig. 3). Lean body water contents of submerged snakes (median, 75.2%), measured after 165 d, were no different (P = 0.376) from those in the initial sample (median, 75.0%), but were much higher (P < 0.001) than those of air hibernators (Fig. 3). Sex had no influence on rate of mass loss (P = 0.202).

Aggregation and activity behaviors of air hibernators were prominently influenced by cage humidity. Group aggregation index increased with increasing cage humidity, whereas group activity index was inversely related to cage humidity (Table 3).

Median dry liver mass, measured at the time of death or sacrifice, was statistically distinguishable (P = 0.003) among the all-male treatment groups (Fig. 4); dry liver masses were greatest in the submerged group (0.311 g), intermediate in the 5°C, 0.16 kPa group (0.250 g), and lowest in the 12°C, 0.21 kPa group (0.174 g). Corresponding fat body masses also followed this trend, but the differences were not statistically significant (P = 0.130). However, group medians for fat body mass were all significantly (P = 0.016) lower than that of the initial sample (Fig. 4). Calculated energy consumption rates, based upon lipid utilization, were highest in the 12°C, 0.21 kPa group, intermediate in the 5°C, 0.16 kPa group, and lowest in the 5°C submerged group (Table 4).

**Discussion**

**Mass loss**

The proportion of prehibernation body mass lost during hibernation in the present study (24.0–31.7%) was much greater than typical values (<10%, Hirth 1966; ca. 13%, Aleksiuk and Stewart 1971; up to 5%, Parker and Brown 1980) reported for snakes hibernating in air, at similar temperatures and under natural conditions. However, snakes in these studies were field collected following emergence and may have rehydrated partially by drinking before being weighed. Larsen (1986) reported that several newly emerged Thamnophis sirtalis parietalis showed some urgency to drink from pools formed by melting ice.

High rates of mass loss in T. sirtalis during simulated hibernation in air were characteristically associated with reduced survival times. Snakes kept at lower VPDs survived relatively longer, indicating that dehydration was an important mortality factor. Still, mass loss rates of several individuals overlapped those of snakes in other treatment groups. This intragroup variation likely reflects differential tendencies among individuals for aggregation and behavioral activity (see later). Under natural conditions, similarly sized conspecifics can differ markedly in the amount of mass lost while hibernating within a particular den (Hirth 1966; Macartney 1985; Charland 1987). Calculations based on the body water content (median, 75% of lean fresh mass) and fat body mass (median, 0.786 g) of snakes in the initial group suggest that in male snakes kept in...
Fig. 2. Changes in body mass, as a percentage of prehibernation body mass, of male garter snakes (N = 8) submerged in 5°C water during laboratory hibernation. Upper and lower boundaries show extremes; heavy line connects group median values.

Fig. 3. Plot of lean body water content versus liver water content (as percentage of fresh mass), showing data for individual snakes exposed to different thermal and humidity regimes during laboratory hibernation, relative to the line of equality. Snakes in the initial group were assayed for lean body water content (range of values indicated by the horizontal bar) before hibernation; other snakes were assayed at the time of their death or sacrifice during hibernation.

Table 3. Indices of behavioral activity and aggregation for garter snakes hibernating in the laboratory under different thermal and humidity regimes

<table>
<thead>
<tr>
<th>Hibernative conditions</th>
<th>Activity index</th>
<th>Aggregation index</th>
<th>No. of observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp. (°C) VPD (kPa)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0.16</td>
<td>2.0</td>
<td>16.1</td>
</tr>
<tr>
<td>5</td>
<td>0.21</td>
<td>2.8</td>
<td>10.1</td>
</tr>
<tr>
<td>5</td>
<td>0.27</td>
<td>4.4</td>
<td>4.3</td>
</tr>
<tr>
<td>5</td>
<td>0.39</td>
<td>5.0</td>
<td>2.3</td>
</tr>
</tbody>
</table>

*Average of the minimum number of individuals changing quadrant location within the ca. 10-d period between observations. Observations were discontinued after the first member of each group died.

*Sum of x²-values, calculated using expected (from random distribution) and average observed distribution frequencies for each of the four cage quadrants. Lower values indicate more random distributions of snakes within the hibernation chambers.

air at 5°C, 90—100% of the observed mass change was due to water loss. The use of stored nutrients therefore contributed little to the overall mass loss in these snakes. In males kept at 12°C, 84—95% of the observed decrease in total body mass was attributed to water loss. The relatively greater proportion of dry mass and lipid lost in this group undoubtedly reflects the higher metabolic rates of these snakes, because nutrient consumption would be more pronounced. However, by the time of their death (median survivorship, 100 d), most snakes in the 12°C group reduced their nutrient stores by only <1 g. Thus, the often significant loss of body mass observed in naturally hibernating snakes (e.g., Hirth 1966; Parker and Brown 1980) probably reflects chiefly water loss. Inferences regarding changes in the nutritional status of hibernating reptiles should therefore be made with care.

Desiccation and mortality

Regardless of experimental treatment, all snakes that succumbed did so when a critical hydration state (pooled median, 65% of lean fresh mass) was reached. Death was due, no
doubt, to the effects of desiccation rather than to starvation, as
significant portions of their fat body stores remained in all
snakes at the time of their death (Table 4). Water in the liver
is conserved during dehydration, probably because of the
internal position of the liver. This result is beneficial because
homeostasis in this organ is vital. Necropsies were not performed
in the present study, but physiological factors likely
effecruating the death of dehydrating snakes include osmotic
stress, acid—base disturbance, and cardiovascular failure
resulting from increased blood viscosity.

Several investigators have suggested that excessive dehydration
may adversely affect the hibernation survival of reptiles
(Maple 1968; Parker and Brown 1973; Brown et al. 1974;
Wasser 1985), and this contention is strongly affirmed by the
results of this study. Only two of the eight snakes subjected
to the most favorable humidity regime (VPD = 0.16 kPa;
85% RH) used in this study survived for 165 d, the typical
period of natural hibernation in the central Wisconsin den. In
nature, reptiles are often closely associated with standing
water, wet substrates, or humid air during hibernation
(Carpenter 1953; Viitanen 1967; Maple 1968; Bauwens 1981;
H. K. Reinert, personal communication), and some appear to
select these situations when a choice is available (Brown et al.
1974; Costanzo 1985). Owing to the differential survivorship
among the treatment groups, a direct comparison of fat body
masses measured at death would have underestimated the magnitude of the differences in energy consump-
tion. Instead, inferences were drawn from rates of fat body
depletion calculated using an estimate (obtained from the
initial group) of prehibernation fat body mass. Significant dif-


effect on internal vapor pressure and by increasing behavioral
activity (Lillywhite 1987).

Behavioral aggregation and activity
Aggregated snakes show reduced rates of water loss relative
to those tested individually (Noble and Clausen 1936; Graves
et al. 1986). Parker and Brown (1973) suggested that this
mechanism may lower winter mortality rates among some
snakes. Accordingly, the aggregations of snakes occasionally
observed within natural dens (see review by Gregory 1982)
are probably formed to reduce cutaneous water loss; there is
apparently no thermogenic advantage to this behavior
(Lillywhite 1987). A reduction in behavioral activity should also
reduce water loss because ventilation frequency would pre-
sumably decline and the boundary layer of moist air would be
less disturbed (Spotila and Berman 1976). Thus, in the present
study these behavioral adjustments were expected to be more
pronounced among snakes kept in drier air. Paradoxically,
snakes kept in drier air were actually more active and
aggregated less than those kept in moister air. These results
likely compounded the influence of the high VPD, thereby
accelerating rates of water loss. Snakes kept in drier air often
appeared restless; greater activity and, consequently, less
aggregation probably resulted because snakes were strongly
motivated to search for water or more humid microsites.
Snakes often move about to thermoregulate within natural
hibernacula (e.g., Sexton and Marion 1981), but movements
apparently unrelated to thermotaxis have also been described
(Drda 1968). It is conceivable that hibernating snakes respond
similarly to the need for conserving body water.

Submerged hibernation
After surviving for 165 d, all submerged hibernators had
lean body water contents similar to those of snakes in the ini-
tial group. This finding agrees with that of Wasser (1985),
who demonstrated that water snakes (Nerodia sipedon)
remain hydrated during submerged hibernation. Snakes sub-
merging in cold water (or perhaps even those that drink ad libi-
tum during winter) are clearly at an advantage because they
remain in water balance during hibernation. In the present
study, submerged individuals gained and lost as much as 5 and
8%, respectively, of their prehibernation mass by the end of
165 d. The significant relationship between final body water
content and the degree (and direction) of mass change suggests
that the latter resulted from slight alterations in hydration
states during winter. Thus, individual differences in osmo-
regulation are apparent even in submerged snakes.

Hibernation energetics
Differences in fat body and dry liver masses, measured at
the time of death or sacrifice, support the hypothesis that body
temperature and submergence behavior strongly influence the
rate of energy consumption in hibernating snakes. Changes in
liver mass have previously been used to show depletion of
glycogen stores during winter (e.g., Dessauer 1953; Aleksiuk
and Stewart 1971), but also reflect the loss of soluble proteins,
an important energy source in T. sirtalis hibernating in Wis-
consin (Costanzo 1985). Owing to the differential survivorship
among the treatment groups, a direct comparison of fat body
and dry liver masses measured at death would have underesti-
mated the magnitude of the differences in energy consump-
tion. Instead, inferences were drawn from rates of fat body
depletion calculated using an estimate (obtained from the
initial group) of prehibernation fat body mass. Significant dif-

FIG. 4. Fat body and dry liver masses of male garter snakes mea-
sured at the time of death or sacrifice during laboratory hibernation.
The height of each bar indicates the group median; vertical lines indi-
cate ranges. Treatment groups are as follows: I, initial (prehiberna-
tion); A, 5°C, submerged in water for 165 d; B, 5°C, 0.16 kPa for
133 d (median); C, 12°C, 0.21 kPa for 100 d (median).
Table 4. Fat body depletion and associated energy metabolism in male garter snakes hibernating in the laboratory under different thermal and humidity regimes

<table>
<thead>
<tr>
<th>Hibernative condition</th>
<th>Temp. (°C)</th>
<th>VPD (kPa)</th>
<th>% depleted at death</th>
<th>Time for 100% depletion (d)</th>
<th>Rate of depletion (mg/d)</th>
<th>Rate of energy consumption (cal/d)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Submerged</td>
<td>5</td>
<td>0.16</td>
<td>48.4</td>
<td>340</td>
<td>2.31</td>
<td>21.5</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.21</td>
<td>53.8</td>
<td>246</td>
<td>3.19</td>
<td>29.7</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td></td>
<td>85.6</td>
<td>117</td>
<td>6.73</td>
<td>62.6</td>
</tr>
</tbody>
</table>

*Calculated from fat body depletion rates and an estimate (9.3 cal/mg) (1 cal = 4.1868 J) of the caloric content of lipid.

The results of the present study suggest that to increase the probability of surviving winter, snakes should locate and occupy the most humid and coldest tolerable den microsites available during hibernation. Snakes can avoid the effects of dehydration by submerging in water or, perhaps, drinking freely during winter. Submerged snakes have an additional advantage because lipids and liver-stored nutrients are conserved, therefore more energy is available for reproductive processes when snakes emerge in spring.

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Male snakes had more than adequate fat body reserves to survive a 165-d winter at 5°C, in either air or water. Calculated lipid consumption rates (Table 4) indicate that those remaining in air would have had only 33% of their fat body remaining after 165 d (had they not died of dehydration), whereas submerged snakes had 52% left. Previous work showed that at 5°C, oxygen consumption in submerged snakes is only half that in snakes kept in air; this difference was ascribed to decreased oxygen availability and reduced behavioral activity during submergence (Costanzo 1989). Differential changes in liver and fat body masses in the present study strongly support this finding

Male snakes kept at 5°C in both media used very small amounts of lipid from abdominal fat bodies during hibernation. This loss would probably have been undetectable by gravimetric means had treatment groups containing females (which have larger and more variable fat bodies) been sampled, or had the all-male groups not been carefully matched for size. Indeed, numerous investigators (e.g., Brown et al. 1974; Costanzo 1985; Wassner 1985) have been unable to show significant changes in fat body mass during winter; the small amount used and high sample variances undoubtedly make the detection of change very difficult.

Conservation of stored nutrients during hibernation is important because snakes inhabiting northern latitudes must begin courtship activities immediately following spring emergence (Gregory 1982). In Manitoba, male T. s. parietalis are engaged in reproductive activities for 4 weeks or more; they do not feed, and high body temperatures (25–29°C) during courtship make this an energetically expensive period (Garstka et al. 1989). Reproductive success therefore seems dependent upon having enough residual energy stores to fuel courtship activities in spring. The cost of mating is much less in females than in males (Crews et al. 1987), though residual energy stores are channeled into the development of embryos and may therefore influence fecundity significantly. In snake populations that occur at high latitudes, insufficient energy reserves apparently preclude annual reproduction in some females (Larsen 1986; Graves et al. 1986).

Snakes kept at 12°C, a probable body temperature of snakes overwintering at lower latitudes (e.g., Drda 1968; Jacob and Painter 1980), depleted their fat bodies much more quickly than those kept at 5°C. According to the calculated rate of depletion, 117 d would be required before male snakes hibernating at 12°C would completely exhaust their abdominal fat body reserves (Table 4). Considering the shorter winter in southern locales, this time period seems adequate.


Maple, W. T. 1968. The overwintering adaptations of Sistrurus c. catenatus in northeastern Ohio. M.A. thesis, Kent State University, Kent, OH.


