

Phenology and ecology of hibernation in spotted turtles (*Clemmys guttata*) near the northern limit of their range

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Abstract: Using mark–recapture techniques, temperature-sensitive radio transmitters, and miniature temperature data loggers we investigated the hibernation ecology of northern temperate zone spotted turtles (*Clemmys guttata*) in Georgian Bay, Ontario, over 4 winters (1993–1997). We observed 18 hibernacula that were occupied by 34 turtles; 11 hibernacula were apparently occupied by single turtles, and 7 were used communally by up to 9 individuals. Hibernacula were located in swamps and were of 2 types: sphagnum moss hummock ($n = 15$) and rock cavern ($n = 3$). Almost half of the individuals (16 of 34) used the same hibernaculum in at least 2 winters. Turtles entered hibernacula between mid-September and October, when their body temperature was between 12 and 16°C, and exited them in mid to late April, when ambient temperatures ranged between 1 and 5°C. A waterproof temperature data logger attached to a turtle indicated that this turtle was protected from freezing in a thermally stable hibernaculum (body temperature range 0.3–3.9°C) despite highly variable (a 37°C change over 5 days) and low air temperatures (minimum –35°C). Loss of body mass (2%) during hibernation was not significant. We observed no mortality within hibernacula over the 4 winters; however, 3 turtles were destroyed by predators near the hibernacula. These data provide insight into the role of climate in limiting the northern distribution of this species.

Résumé : Nous avons étudié l'écologie de l'hibernation chez des Tortues ponctuées de la zone tempérée nord (*Clemmys guttata*), dans la baie Georgienne, Ontario, au cours de 4 hivers (1993–1997) en utilisant des techniques de capture-recapture, des émetteurs radio sensibles à la température et des mini-thermomètres enregistreurs. Nous avons observé 18 hibernaculum occupés par 34 tortues; 11 semblaient occupés par des tortues seules et 7 étaient communautaires, utilisés par un maximum de 9 individus. Les hibernaculum étaient dans des marécages et on pouvait en reconnaître 2 types : des buttes de sphagnes ($n = 15$) et des cavernes rocheuses ($n = 3$). Près de la moitié des tortues (16 sur 34) ont utilisé le même hibernaculum durant au moins 2 hivers. Elles gagnaient leur hibernaculum entre la mi-septembre et le début d'octobre, alors que leur température corporelle était entre 12 et 16°C, et le quittaient entre la mi-avril et la fin d'avril, alors que les températures ambiantes se situaient entre 1 et 5°C. Un relevé de données de température à l'épreuve de l'eau attaché à une tortue a révélé que cette tortue était protégée des températures de gel dans un hibernaculum thermiquement stable (température du corps de 0,3–3,9°C), en dépit de températures ambiantes très variables (variation de 37°C sur une période de 5 jours) et parfois très basses (–35°C). La perte de masse (2%) encourue au cours de l'hibernation n'était pas significative. Nous n'avons enregistré aucun cas de mortalité au cours des 4 hivers; cependant, 3 tortues ont été victimes de prédateurs près de leur hibernaculum. Ces données jettent de la lumière sur le rôle que joue le climat en imposant des limites à la répartition de cette espèce.

[Traduit par la Rédaction]

Introduction

Reptiles living in environments with long cold winters that inhibit feeding must depress their metabolic rate and reduce energy expenditure throughout winter; thus, hibernation is a major feature of the annual cycle of temperate-zone

reptiles. Some aspects of hibernation, such as the availability of suitable hibernacula that protect animals from freezing, the restricted space within hibernacula (Gregory 1982), and severe metabolic acidosis as a result of prolonged submergence in hypoxic water (Ultsch and Jackson 1982), may limit the northern distribution and abundance of these species. In addition, the length of winter may indirectly limit the northern distribution of reptiles if the active season is too short to allow them to complete the reproductive cycle (Licht 1972; Bohn and Brooks 1994; Brown and Brooks 1994). At the northern extremes of their ranges, freshwater turtles may spend more than half of their lives in hibernation (Ultsch 1989).

The spotted turtle (*Clemmys guttata*) is restricted to eastern North America. It ranges from Ontario, Quebec, and Maine southward along the Atlantic Coastal Plain to central

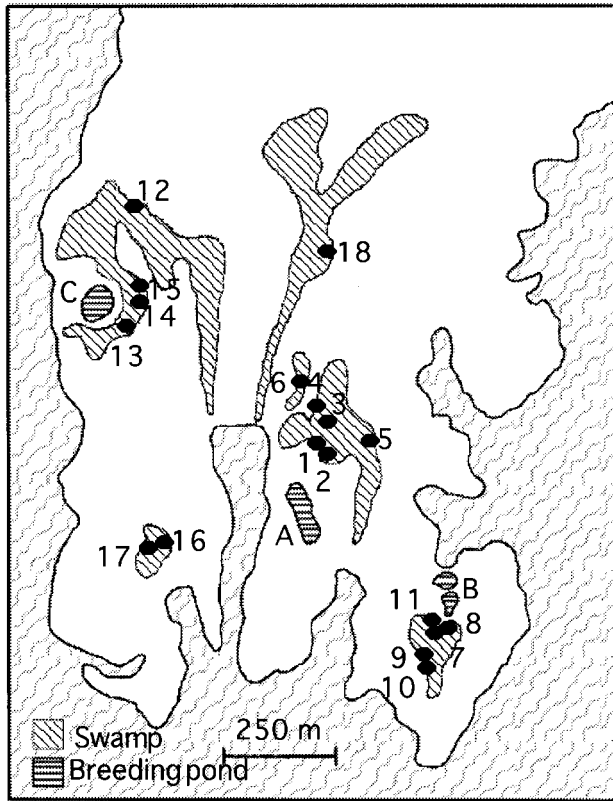
Received November 18, 1998. Accepted May 6, 1999.

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Fig. 1. Map of the study site in Georgian Bay, Ontario, showing the spatial relations of spotted turtle (*Clemmys guttata*) hibernacula (1–18) located in swamps, and communal breeding ponds (A–C). Distances implied by the spacing of symbols among sites are not to scale. A maximum–minimum air-temperature thermometer was located at pond A.



Florida and westward to Illinois (Ernst et al. 1994; Barnwell et al. 1997). Known aquatic hibernation sites of spotted turtles include muskrat (*Ondatra zibethicus*) burrows in stream banks (Ernst 1982; Behler 1996), vernal pools and puddles (Ward et al. 1976; Perillo 1997), sphagnum swamps (Legere 1987; Graham 1995; Behler 1996; Perillo 1997), cattail marshes (Wilson 1994), and vegetative mats of alkaline fens (Lewis and Ritzenthaler 1997). Terrestrial hibernation has been suggested (Netting 1936) though not confirmed. Spotted turtles can remain active at low ambient temperatures (Ernst 1976, 1982; Litzgus and Brooks 2000) and are often the first among syntopic chelonians to emerge from hibernation (Ward et al. 1976; Belmore 1985, 1990; Ultsch 1989).

Other aspects of the winter biology of this species, including physical features and fidelity to hibernacula, microenvironmental conditions, thermal tolerance, and physiological changes promoting winter survival, are virtually unknown (Lewis and Ritzenthaler 1997). Few studies have followed individual turtles over several years of hibernation (Brown and Brooks 1994; Lewis and Ritzenthaler 1997). The purpose of this investigation was to describe the hibernation phenology and ecology of northern spotted turtles.

Information on the physical properties of hibernacula, especially temperature, over-winter mortality, changes in body mass, site fidelity, and the use of communal hibernacula is important to understanding winter adaptations and the role of climate in limiting northern distributions of reptiles. Such information assists in the creation and implementation of conservation programs that set aside areas in order to maintain viable populations of spotted turtles, which are currently considered “vulnerable” in Canada (Oldham 1991).

Materials and methods

Study site

This study was conducted over 4 consecutive winters (1993–1997) on a 300-ha island near the east shore of Georgian Bay, Ontario (45°N, 80°W). The climate of the Georgian Bay area is characterized by long (7–8 months) cold winters and short, relatively cool summers. The island is predominantly composed of low-lying acidic swamps interspersed among Precambrian granite rock outcrops. Rock outcrops are sparsely vegetated with white pine (*Pinus strobus*) and juniper (*Juniperus communis*), whereas the swamps are abundantly vegetated with sphagnum moss (*Sphagnum* spp.), ferns (*Osmunda cinnamomea*, *O. regalis*), hydrophilic shrubs (*Nemopanthus mucronata*, *Alnus rugosa*, *Myrica gale*), and trees (*Acer rubrum*, *Quercus rubra*, *Q. alba*, *Larix laricina*). The island is relatively undisturbed, as it has no human dwellings or roads and is bordered by a provincial fish sanctuary. Data reported herein were collected as part of an ongoing capture–recapture study that began in 1977 (Bird 1982²; Litzgus 1996; Litzgus and Brooks 1998a, 1998b, 2000).

Animal observations

Observations of turtle hibernation behaviour were made within a 1-km² area at the southern end of the study island. This area included a beaver (*Castor canadensis*) pond (~3500 m²) in which many of the turtles mated (pond A; Fig. 1), 2 other communal breeding areas (ponds B and C; Fig. 1), adjacent rock outcrops upon which turtles nested in June and aestivated in July and August (Litzgus and Brooks 2000), and 5 swamps containing 18 known hibernacula (Fig. 1). A few additional swamps (not depicted in Fig. 1) were present on the study site but were not searched for hibernating spotted turtles. The study site was visited weekly in September and at 2-week intervals during October–November, at which time we collected information on turtle location, activity status, body mass, ambient temperature, body temperature, and date of entrance into hibernacula. Owing to its remote location, the study island could not be visited during winter, but excursions were made to the site in spring (typically late April) of 1994, 1995, and 1997, after ice in Georgian Bay had melted. During spring visits we determined whether turtles had emerged from hibernation, weighed captured turtles, and subsequently followed turtles to their breeding areas.

We observed hibernation behaviour of 32 marked adult turtles (15 females, 17 males), 1 marked juvenile, and 1 uncaptured and therefore unidentified juvenile. Most of these turtles were observed in more than 1 winter, therefore we made 64 observations of hibernation behaviour. Turtles were encountered opportunistically or located using radiotelemetry (Litzgus and Brooks 1998a), which allowed us to both locate turtles and estimate their body temperatures (T_b). In 1993–1994, 11 turtles (6 females, 5 males) were outfitted with temperature-sensitive radio transmitters (Holohil Systems Inc., Woodlawn, Ont.). In 1994–1995, we monitored 6

²G. Bird. 1982. Observations on the population ecology of the spotted turtle, *Clemmys guttata*, near the northern limit of distribution. Hons. B.Sc. thesis, Trent University, Peterborough, Ont.

turtles (4 females, 2 males) that were outfitted with temperature-sensitive radio transmitters; 5 of these had been tracked during the previous field season. Transmitter temperatures were obtained at the outset of each radiolocation event for each turtle to minimize disturbance. The amount of time (in seconds) required for 10 signal pulses was recorded, and temperature was interpolated from calibration curves for each transmitter. In 1996–1997, we monitored T_b of a 270-g male throughout the winter using a waterproof miniature data logger (TidbiT®, Onset Computer Corporation, Pocasset, Mass.) that was attached by epoxy to the rear surface of his carapace. In this study we assumed that transmitter and data-logger temperatures were reasonably accurate estimates of turtle T_b , particularly because turtles were within thermally stable hibernacula (Brown 1992; Brown and Brooks 1994).

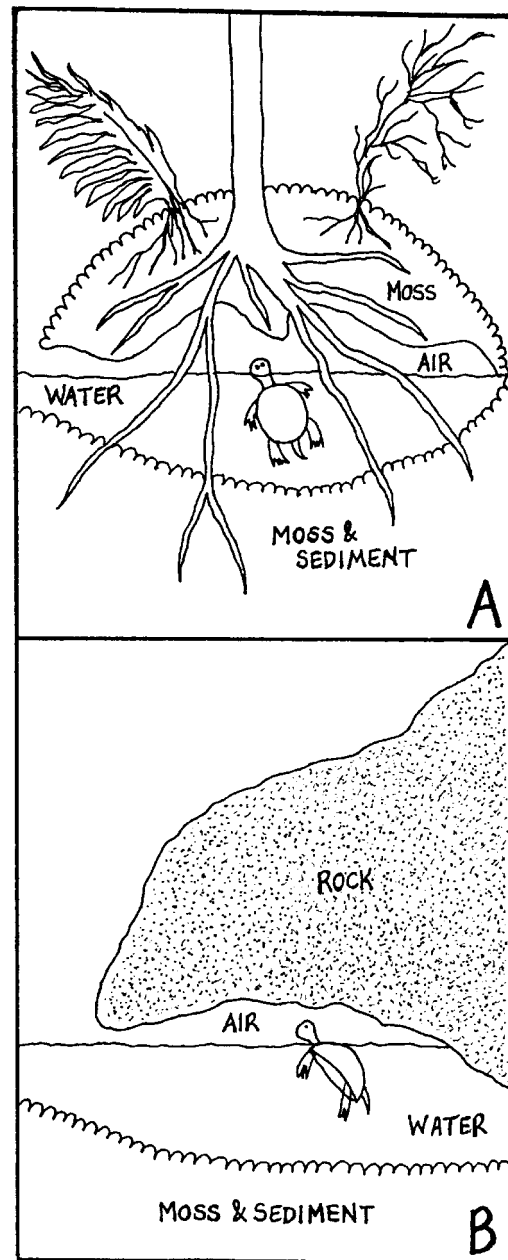
The body mass lost during hibernation was determined for adult turtles during the winters of 1993–1994 ($n = 8$), 1994–1995 ($n = 11$), and 1996–1997 ($n = 6$). Prehibernation masses were obtained between 28 September and 20 November upon, or shortly after, entrance into hibernacula. In the spring of 1994 and 1995, post-hibernation masses were obtained between late April and early May (“early spring”), just after emergence from hibernacula, when cold water presumably prevented turtles from feeding (Ernst 1982), and again in mid-May (“midspring”) of those 2 years plus 1997, when turtles had reached the breeding areas and may have begun feeding. Pre-hibernation masses were compared with both early and mid spring post-hibernation masses using repeated-measures ANOVA and Bonferroni multiple comparisons, except for 1996–1997, for which we used a one-tailed paired t test because we had post-hibernation mass data only for midspring.

Our research was carried out under the guidelines of the Canadian Council on Animal Care and University of Guelph Animal Care Protocol Nos. 93R019, 94R019, and 96R098.

Hibernation environment

Minimum air temperature was recorded during the first 3 winters (1993–1996) using a maximum–minimum thermometer (Fisher, Pittsburgh, Pa.) located at a breeding area (pond A; Fig. 1) approximately 100 m from a swamp containing 6 known hibernacula. During winter 1996–1997, field temperatures were recorded at 1-h intervals using miniature data loggers (Hobo®, Onset Computer Corporation). Eight data loggers were deployed to characterize environmental temperatures associated with 4 hibernacula (sites 1, 6, 7, and 12; Fig. 1) that were located by radio-tracking turtles. However, most of the data loggers were damaged by mammals. Therefore, we obtained complete temperature records only from 2 units placed at a single hibernaculum (site 1) where the turtle outfitted with the waterproof data logger hibernated in all 4 winters of the study. These 2 data loggers recorded the air temperature 1.5 m above the top of the hibernaculum, and the temperature of the swamp surface 0.5 m from the hibernaculum’s access hole. The “swamp-surface” unit was placed in a waterproof case (Onset Computer Corporation) outside the hibernaculum. The cylindrical case (diameter 5.5 cm, length 10.5 cm) was painted mottled green and brown to mimic the colours of the substrate and vegetation. When the swamp was dry in early autumn, this unit rested on the vegetative mat and therefore recorded the temperature of the substrate. When autumn rains inundated the site, this unit floated and therefore measured the temperature of the water surface outside the hibernaculum. In winter this unit was presumably encased in ice or covered in snow. When the data loggers were deployed (28 September 1996), we measured the temperature and dissolved oxygen concentration (YSI 55) of the water within each of the 4 representative hibernacula and recorded descriptions of their physical characteristics (type of hibernaculum, chamber dimensions, and water depth).

Fig. 2. Diagrammatic representation of the two types of hibernacula used by spotted turtles (*C. guttata*) in Georgian Bay, Ontario: hummock (A) and rock cavern (B). The horizontal axis of the frame represents approximately 1 m.

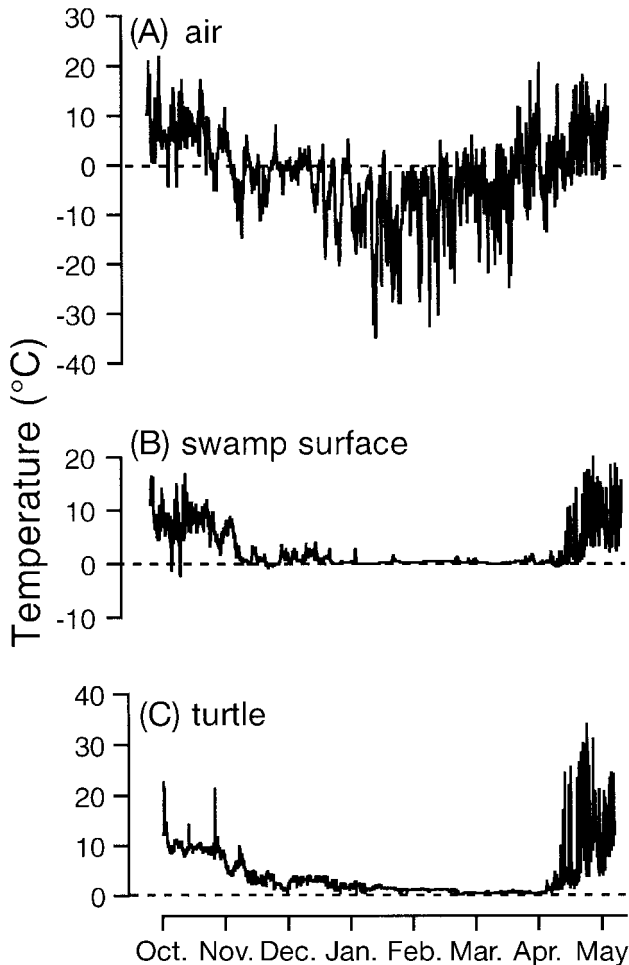


Results

Hibernation environment

We identified a total of 18 spotted turtle hibernacula dispersed throughout 5 swamps at the study site (Fig. 1). The swamps are characterized by channels of water winding among elevated islands of sphagnum moss. There were 2 types of hibernacula: hummock ($n = 15$) and small rock cavern ($n = 3$). Hummock hibernacula consisted of an open pocket under an elevated island of thick sphagnum moss reinforced by the roots and stems of ferns, small shrubs, and

Fig. 3. Temperature records obtained from data loggers positioned in a swamp in Georgian Bay, Ontario, at a communal spotted turtle (*C. guttata*) hibernaculum (site 1; Fig. 1) throughout the winter of 1996–1997. (A) Air temperature 1.5 m above the hibernaculum. (B) Swamp-surface temperature 0.5 m outside the hibernaculum exit hole. (C) Body temperature of a male spotted turtle known to have hibernated in the site in 4 consecutive winters.



trees (Fig. 2A). Typically the chamber was accessed by 1–4 tunnels whose external openings (10–20 cm in diameter) were located near the base of the 1–2 m diameter hummock. Hummock hibernacula were located at the shore or within the main body of swamps. Rock cavern hibernacula were located at a swamp's edge, where an extension of a massive granite outcrop jutted downwards from shore into the swamp (Fig. 2B). This configuration created a chamber that turtles accessed from the swamp through any of 1–3 tunnels.

Both types of hibernacula contained standing water when turtles were found inside them, but may or may not have had an air space, depending on seasonal water levels. They presumably contained water throughout winter but, like the swamps themselves, were almost dry during much of the summer. Water depth within hibernacula during October and April was typically 30–40 cm. Although turtles in hibernacula were found under water in autumn, they may have had access to air (Fig. 2) for breathing within the hibernaculum

chamber during winter, if the water surface did not ice over completely.

The minimum air temperature during the 4 winters (1993–1997) was $-33 \pm 2^\circ\text{C}$ (mean \pm SE; range -37 to -27°C). In midwinter 1996–1997, the air temperature fluctuated by as much as 37°C (-35 to 2°C ; Fig. 3A) over a 5-day period, whereas T_b of the turtle (Fig. 3C) was remarkably stable, remaining between 1 and 2°C during the same interval. T_b remained relatively constant during January–March (Fig. 3C), whereas the air temperature fell below -20°C on at least 16 occasions during this period (Fig. 3A). T_b was lowest (range 0.3 – 1°C) from the last week of February until the first week of April.

The temperature of the swamp surface outside the hibernaculum (Fig. 3B) closely tracked the air temperature during October and the first half of November (Fig. 3A), which suggests that there was little or no standing water in the swamp at that time, particularly because the temperature fell below 0°C twice. The reduced fluctuation in temperature outside the hibernaculum in late November (Fig. 3B) probably reflects the inundation of the swamp as a result of heavy autumn rains. By January the data logger was likely encased in ice or covered in snow, as the fluctuations in temperature deviate little from 0°C (Fig. 3B).

A diurnal pattern in turtle T_b values became evident in April, concomitant with increasing air temperatures that likely melted ice and snow in the swamp (Fig. 3). The turtle apparently began basking outside the hibernaculum during the second week of April, as its maximum T_b (Fig. 3C) during the day ($>25^\circ\text{C}$) exceeded that of the air temperature (Fig. 3A). During this period, the turtle likely returned to the hibernaculum or submerged in the swamp at night, as T_b values during the night remained well above air temperatures, which often fell below 0°C .

In autumn (28 September 1996), dissolved oxygen (DO) concentrations of water within hibernacula were low and varied little (range 1.0–2.2 ppm) among 4 sites (2 hummock type, 2 rock cavern type). In spring (10 May 1997), DO concentrations within hibernacula were slightly higher (3.3–4.7 ppm).

Phenology of hibernation

Entrance

In late summer of each year, most turtles were buried under vegetation on rock outcrops or in other upland areas (Litzgus and Brooks 2000) peripheral to the swamps in which they subsequently hibernated. By late August, some turtles were buried in leaf litter in an upland area immediately adjacent to the swamp in which hibernation subsequently occurred, whereas others were in the swamps, moving among known and (or) apparent hibernacula. Some turtles repeatedly moved back and forth between upland forms and aquatic hibernacula and (or) sites that resembled aquatic hibernacula. These movements continued into September, and sometimes October, at which time turtles entered and remained in hibernacula. The hibernaculum chosen for overwintering was typically within 50 m of a turtle's upland form and 100 m of its breeding area (note that most spotted turtles at this site return to the same breeding pond every year).

The final T_b recorded before turtles entered their hibernacula was $15.8 \pm 1.6^\circ\text{C}$ ($n = 9$) in 1993 and $16.1 \pm 1.8^\circ\text{C}$ ($n = 6$) in 1994. These means were not significantly different ($t = 0.09$, $df = 13$, $P = 0.9$). Similarly, T_b of turtles at the time they were first found in a hibernaculum did not differ between 1993 ($12.1 \pm 0.7^\circ\text{C}$, $n = 10$) and 1994 ($12.6 \pm 0.7^\circ\text{C}$, $n = 6$; $t = 0.4$, $df = 14$, $P = 0.7$). On 28 September 1996, when 14 turtles were found in hibernacula, the water temperature within these hibernacula ranged from 13.1 to 13.9°C and corresponding air temperatures ranged from 11 to 15°C .

Emergence

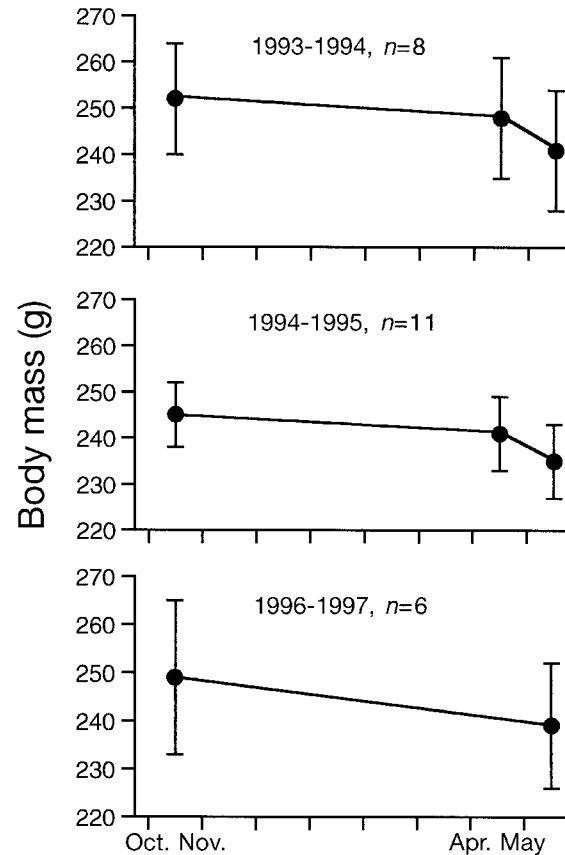
Each spring, most turtles had emerged from their hibernacula by the time the study site became accessible in late April. Thus, we could not determine the earliest emergence dates; however, turtles presumably emerged from hibernation in mid-April. The sudden increase in T_b of the turtle outfitted with the waterproof data logger during the second week in April (Fig. 3C) suggests that it emerged from its hibernaculum at this time. Owing to the inaccessibility of the study site in winter, we can only presume that turtles remained within their hibernacula until spring. In no case did we find in spring a turtle within or near a hibernaculum other than the one it had entered in the previous autumn. On 20 April 1995, we observed 6 of 9 turtles outside of, but <1 m from, their hibernacula of the previous autumn. The remaining 3 turtles were still within their hibernacula. The air temperature was approximately 4°C and the water temperature outside hibernacula was approximately 2°C . T_b , estimated using radiotelemetry, was 2.1°C for a turtle remaining within a hibernaculum, and 4.1°C for a turtle resting in water near the opening of its hibernaculum. These temperatures support the contention that spotted turtles emerge from hibernation at a very low T_b (Ernst 1976; Ward et al. 1976; Belmore 1985, 1990; Legere 1987).

Mortality and decrease in body mass over winter

Mortality associated with overwintering was monitored opportunistically when we surveyed hibernacula in autumn and spring. In spring 1994, we found 2 depredated adults: the shell remains of a male, and a severely injured female (who died 11 days later), both near the same hibernaculum (site 11; Fig. 1). In autumn 1994, we found the remains of one (telemetered) adult male scattered on a rock outcrop adjacent to the site 13 hibernaculum (Fig. 1) within which we located him during the 2 previous visits, and where he had hibernated the previous winter. Potential predators of spotted turtles at the study site include raccoon (*Procyon lotor*), otter (*Lutra canadensis*), red fox (*Vulpes vulpes*), and black bear (*Ursus americanus*). Of 64 observations of hibernation behaviour over 4 winters, no known mortalities occurred within hibernacula.

Decreases in body mass associated with hibernation were monitored over 3 winters (Fig. 4). Mass losses between entrance into hibernacula (October–November) and arrival at breeding ponds (mid-May) were small (4%) but significant in all 3 winters (1993–1994: $F_{[2,23]} = 8.33$, $P < 0.01$; 1994–1995: $F_{[2,32]} = 7.85$, $P < 0.01$; 1996–1997: $t = 2.02$, $df = 5$, $P < 0.05$). However, between entrance into and exit from hiber-

Fig. 4. Body mass (mean \pm SE) of spotted turtles (*C. guttata*) before and after hibernation over 3 winters in Georgian Bay, Ontario. Pre-hibernation masses were obtained in October–November. Post-hibernation masses were obtained upon exit from hibernacula in late April – early May (“early spring”) and again when turtles had migrated to breeding ponds in mid-May (“midspring”).



nacula (late April), losses were smaller (2%) and not significant (Bonferroni multiple comparison, $P > 0.05$).

Site fidelity and communal hibernation

Twelve of the 34 turtles observed in this study were monitored during 1 winter. Observations of the remaining 22 turtles, which were monitored for 2–4 winters, provide unique insight into fidelity to hibernacula and interindividual variation in hibernation behaviour of this species (Table 1). Of the 22 turtles monitored in ≥ 2 winters, all but 1 showed annual fidelity to a complex of hibernacula (i.e., a swamp; Fig. 1), and many turtles used the same hibernaculum each winter. One individual used site 1 in 4 consecutive winters and 15 others used the same hibernaculum in ≥ 2 winters during the study (Table 1). However, 8 of 22 turtles (36%) observed in ≥ 2 winters used different hibernacula. Four turtles switched from one communal hibernaculum to another, 2 turtles switched between hibernating communally and alone in different hibernacula, and 2 turtles hibernated alone in different hibernacula over 2 winters. Overall, no obvious pattern of fidelity to hibernacula could be discerned.

Of the 18 hibernacula monitored during this study, at least 7 were simultaneously occupied by 2 to at least 9 spotted

Table 1. Fidelity of spotted turtles (*Clemmys guttata*) to specific hibernation sites (see Fig. 1) in Georgian Bay, Ontario, during 4 winters.

Turtle ID No.	Sex	Hibernation site used			
		1993–1994	1994–1995	1995–1996	1996–1997
2	F	1	1	1	—
3-7L	F	1	1	—	—
6	M	13	13	—	—
7-7L	F	18	18	—	—
9	M	—	11	—	8
19-6R	F	2	2	1	1
24	M	—	12	—	12
47	M	—	8	—	8
60	M	—	7	—	7
74	M	9	5	—	—
77	F	—	7	—	7
107	F	—	12	—	12
220	M	1	1	1	1
407	M	1	1	1	—
420	M	—	12	—	12
711	F	3	6	—	—
1020	M	14	15	—	—
1070	M	2	1	1	—
4401	F	16	17	1	—
7004	M	2	2	—	—
7010A	F	7	11	—	—
7010B	M	—	7	—	7

Note: Data are shown only for the 22 turtles for which more than 1 winter's data were available; 12 turtles were observed in only 1 winter. A dash indicates that the turtle was not observed in that winter.

Table 2. Numbers of spotted turtles (*C. guttata*) known to have occupied communal hibernacula in Georgian Bay, Ontario, during 4 winters.

Site No.	Type	1993–1994	1994–1995	1995–1996	1996–1997
1	Rock cavern	4 (2F, 2M)	5 (2F, 3M)	9 (3F, 3M)*	2 (1F, 1M)
2	Rock cavern	3 (1F, 2M)	2 (1F, 1M)	—	—
6	Hummock	—	2 (1F, 1M)	—	0
7	Hummock	1 (F)	6 (3F, 3M)	—	6 (4F, 2M)
8	Hummock	—	1 (M)	—	2 (2M)
11	Hummock	—	4 (1F, 2M, 1J)	—	—
12	Rock cavern	—	3 (1F, 2M)	—	4 (1F, 2M, 1J)

Note: The numbers of turtles shown are minimum estimates, since it is possible that we did not detect all turtles present. A dash indicates that the site was not surveyed that winter. The numbers of individuals of each sex are given (F, female; M, male; J, juvenile). Hibernacula 3, 4, 5, 9, 10, and 13–18 were apparently occupied by single turtles in a given winter and are therefore not included in this table.

*Only 6 of these 9 turtles were captured and their identification codes and sex recorded.

turtles (Table 2). Turtles did not appear to segregate by sex among hibernacula (Table 2). Males were found hibernating alone on 8 occasions and females were found alone on 7 occasions; all these sightings were of turtles in hummock hibernacula. These individuals had a propensity for hibernating alone, as they were rarely observed hibernating in the company of other turtles. Turtles hibernating alone did not appear to use smaller, more restricted hibernacula, but we did not measure the dimensions of all sites. None of the syntopic turtle species (*Chelydra serpentina*, *Chrysemys picta*, *Emydoidea blandingii*, *Graptemys geographica*, and

Sternotherus odoratus) or other reptiles (e.g., *Sistrurus catenatus*, *Thamnophis sirtalis*) shared hibernacula with spotted turtles.

Discussion

Hibernation environment

Georgian Bay spotted turtles hibernated aquatically in small rock caverns and under sphagnum hummocks in swamps very similar to those used by this species in Massachusetts (Graham 1995). Elsewhere, spotted turtles hibernate

in muskrat burrows and lodges in the banks of streams that never freeze completely (Ernst 1982; Behler 1996). Although muskrat burrows and lodges were present at the study site along the shores of some bays and in one of the breeding ponds (pond A; Fig. 1), our searches of these sites suggested that spotted turtles did not hibernate in them. Perhaps these sites were avoided because the shallow inland swamps thaw earlier in the spring, allowing turtles to become active sooner and thereby maximize their reproductive output in the short period of frost-free days available at this northern locale. Because turtles must quickly recover acid-base balance by thermoregulating as soon as they emerge in spring (Ultsch et al. 1985; Brown and Brooks 1994), early emergence would be beneficial.

Unfortunately, we could not routinely measure the T_b of turtles during hibernation. However, the turtle outfitted with a waterproof data logger provided some insight concerning the relationships between T_b and the air and water temperatures outside the hibernaculum. T_b remained stable during January–March, perhaps reflecting immobility in thermally stable water, and remained just above the freezing point of the animal's tissues (approximately -0.6°C ; Costanzo et al. 1995) throughout winter. Whether spotted turtles are exposed to temperatures low enough to cause tissue freezing during some winters is not known. Other members of the Emydidae (e.g., *C. picta*, *Terrapene carolina*, and *Terrapene ornata*), whose center of geographic distribution is at a higher latitude than that of any other turtle family (Conant and Collins 1991; Ernst et al. 1994; Holman and Andrews 1994), are adapted to tolerate the freezing of their tissues (Storey et al. 1988; Costanzo and Claussen 1990; Costanzo et al. 1995), but the freeze-tolerance status of spotted turtles is as yet untested. Freeze-tolerance is not necessarily required for survival at northern latitudes, because the T_b values for northern *C. serpentina*, a freeze-intolerant species, were also very low (range 0 – 4°C ; Brown and Brooks 1994). In more temperate locales, spotted turtles may hibernate at higher temperatures that prevent them from freezing. In Pennsylvania, for example, cloacal temperatures of 21 spotted turtles hibernating in muskrat burrows ranged from 4.0 to 15.0°C , while corresponding air and water temperatures ranged from 0.0 to 23.0°C and from 2.0 to 14.2°C , respectively (Ernst 1982).

In autumn, water within hibernacula used by spotted turtles was extremely hypoxic. Water within overwintering sites used by *C. picta* (e.g., Taylor and Nol 1989; St. Clair and Gregory 1990; Crawford 1991), a species that hibernates at the bottom of permanent ponds and marshes, had relatively higher DO concentrations in late autumn (10 ppm in November) and these concentrations were maintained into December (6–12 ppm). In one study, DO approached our low values in January only after ice covered hibernation ponds (2.6 ppm; Taylor and Nol 1989). In an ice-covered Ontario lake in which *C. serpentina* hibernated, DO concentrations ranged from 6.6 to 12.6 ppm (Brown and Brooks 1994). The large amounts of decaying vegetation, coupled with the shallow, relatively stagnant water of the sphagnum swamps, likely explain the comparatively low DO concentration in spotted turtle hibernacula in autumn. Whether spotted turtles are particularly tolerant of environmental hypoxia or obtain

oxygen by breathing air within the hibernaculum chamber remains to be determined. Our autumn observations suggest that turtles had access to air within hibernacula. However, if the water within hibernacula rises to fill the air space during winter, or if it becomes ice-covered like the water outside the hibernacula, then turtles would not have access to air for breathing. This scenario would require that the hypoxia tolerance of the spotted turtle rivals that of *C. picta* (Ultsch and Jackson 1982). In Maryland, spotted turtles hibernated near the edge of vernal pools under water 10–15 cm deep, where they avoided freezing (Ward et al. 1976) and perhaps maximized oxygen uptake (Pinder 1998).

Phenology of hibernation

Generally, spotted turtles spent 7–8 months in their hibernacula, entering in September or October and emerging during mid to late April. Turtles remained near their hibernacula for about 1 week after emergence. They then migrated to breeding areas, arriving by mid-May.

In reptiles, entrance into hibernation may be triggered by exogenous factors such as decreases in food availability, ambient temperature, and photoperiod or by endogenous circannual rhythms (Licht 1972; Gregory 1982; Ultsch 1989). Diminished food availability and consumption likely were not proximate stimuli for spotted turtles in this study, as they had reduced their feeding activity weeks earlier while quiescent in upland forms (Litzgus 1996). Data from temperature-sensitive transmitters and miniature data loggers suggest that entrance into hibernacula was associated with turtle T_b values of approximately 12 – 16°C . Perhaps the inability to achieve optimal T_b during this time of year is a cue for turtles to enter hibernation. Precipitation may also trigger entrance into hibernation for some reptiles (Gregory 1982). During the relatively dry autumn of 1997, hibernacula were unoccupied on 6 and 7 September, at which time the swamps were completely devoid of standing water. Turtles apparently avoid the swamps when they lack standing water and remain instead in upland forms until autumn rains inundate hibernacula.

Some turtles moved between upland areas and swamps for a brief period prior to entering hibernation. These short movements may indicate that turtles were searching for a hibernaculum to which they could commit themselves for the entire winter. Other studies report fall activity of reptiles at hibernacula prior to entrance (see review by Gregory 1982). This activity may help to purge the gut before hibernation (Saint Girons and Saint Girons 1956), or it may be related to the reproductive cycle (Tinkle 1962); however, the advantages of remaining active during the period of prehibernation aphagia remain unclear.

Mortality and decrease in body mass over winter

The results of this study do not support the contention that hibernation is a limiting factor in the northern distribution of turtles, because we found no mortality directly associated with hibernation in our 4-year study. Furthermore, we observed little loss of body mass over winter, which suggests that hibernation is not energetically demanding. We found 1 dead turtle before hibernation and 2 dead turtles after emergence; all 3 had been damaged and perhaps killed by preda-

tors. There is considerable evidence that turtles are most susceptible to predation immediately following emergence from hibernation (Ultsch 1989). Physiological stress increases with duration of submergence in cold turtles. Not only do low temperatures slow the behavioural responses of turtles, but hypoxia results in large perturbations of acid–base and ionic balance, making turtles lethargic and therefore easy prey (Ultsch and Jackson 1982; Ultsch 1989). For example, in a northern population of *C. serpentina*, 34 hibernating turtles were killed by otters over 2 winters (Brooks et al. 1991). There was no evidence that these turtles died from freezing or from other causes while hibernating (Brown and Brooks 1994).

Despite the long hibernation period, surprisingly little loss of body mass (4%) occurred between autumn and mid-May, again suggesting that hibernation does not limit the northern distribution of this species. Turtles lost as much body mass in the few weeks after emergence (2%) as they did over the entire 7 months of hibernation. In fact, mass was lower in mid-May than at any other time during the active season (J.D. Litzgus, unpublished data). Reptiles typically lose <10% of their initial body mass during hibernation, which parallels the reduction in lipid and glycogen reserves (Derickson 1976; Gregory 1982). Some reptiles may lose significant amounts of mass (Congdon et al. 1979; Parker and Brown 1980) and use significant quantities of liver glycogen (Agid et al. 1961; Duguay 1963) during aphagic periods just before and after hibernation. In garter snakes (*Thamnophis sirtalis*), most energy consumption associated with hibernation occurs during the initial and final phases rather than during midwinter (Aleksiuk and Stewart 1971; Costanzo 1985). Because fat storage plays a role in reproduction, decreases in lipid levels following emergence from hibernation occur in most reptiles that mate in spring (Derickson 1976; Gregory 1982).

The inability to detect a significant loss of mass in our turtles during hibernation (autumn to late April) may be due, in part, to an accumulation of water by submerged turtles as a result of reduced kidney function (Ultsch 1989; Brown 1992). Therefore, the additional loss detected between late April and mid-May may be due to turtles excreting accumulated water during the few weeks after emergence from hibernation. Alternatively, post-emergence mass loss may be associated with the turtles' inability to feed when water temperatures are low (<15°C; Ernst 1982) and their concomitant need to expend energy during migration to breeding ponds.

Site fidelity and communal hibernation: conservation implications

Georgian Bay spotted turtles hibernated in groups or alone, and some individuals used different hibernacula over the 4 winters of study. Changing to a different hibernaculum did not appear to be associated with a tendency to hibernate alone, as 6 of the 8 turtles that changed sites hibernated communally in at least 1 winter. Indeed, there was individual variation in hibernation behaviour and no apparent pattern in use of hibernacula. Nevertheless, all but 1 turtle showed fidelity to a complex of hibernacula, and many turtles showed fidelity to specific hibernacula. Similarly, congeneric bog turtles (*Clemmys muhlenbergii*) often return to the same

overwintering sites (Chase et al. 1989; Behler 1996), and sometimes hibernate communally with spotted turtles (Behler 1996). *Chelydra serpentina* from Ontario also show annual loyalty to hibernation areas (Brown and Brooks 1994).

Among reptiles, the degree of annual fidelity to hibernacula reflects the distance between suitable hibernacula: lower fidelity and greater interchange occur where hibernacula are close together (Gregory 1982). In addition, determining whether turtles return to the same hibernaculum can be somewhat subjective unless the hibernaculum is a defined structure, such as the rock caverns and hummocks at the Georgian Bay site. For turtles that hibernate at the bottom of lakes and ponds, it is difficult to conclude whether a specific site is chosen in subsequent winters, despite the obvious choice of an area or complex of hibernacula. Regular use of specific hibernacula may reflect a shortage of suitable sites and may be most common in areas with harsh winters; reptiles in more moderate climates are less threatened by exposure to frost and therefore should find suitable overwintering sites more easily (Gregory 1982). In addition, northern reptiles tend to hibernate communally, whereas southern conspecifics may not (Gregory 1982; Brown and Brooks 1994). Presumably, over-winter survival in a given year encourages return to the same hibernaculum, and communal sites may be established when conspecifics follow the original occupant during subsequent visits.

Communal hibernation in reptiles may be a result of suitable hibernacula being a limited resource (Gregory 1982; Ultsch 1989). It does not appear that suitable hibernacula were limiting at the study site, as each of the 5 swamps studied contained numerous sites that apparently would serve as hibernacula, particularly of the hummock type. Apparently useable hibernacula often go unused in any winter, even in northern regions (Gregory 1982). A study conducted in Ohio suggests that temperature is not the reason for spotted turtles to avoid some potential hibernacula, as temperatures within used and unused hibernacula did not differ (Lewis and Ritzenthaler 1997).

Communal hibernation in reptiles may also occur to facilitate mating by increasing opportunities to find mates and (or) to improve fitness by synchronizing emergence (Gregory 1982; Ultsch 1989). Mating typically occurred in ponds to which turtles migrated from hibernacula. Therefore, communal hibernation by Georgian Bay spotted turtles does not appear to facilitate mating, as mating was rarely observed outside of ponds. All turtles arrived at breeding ponds at about the same time (mid-May), which suggests that emergence is synchronized. However, the presence of conspecifics is not necessary to cue this emergence because turtles hibernating alone arrived at ponds at about the same time as those hibernating communally. Perhaps communal use of hibernacula by Georgian Bay spotted turtles indicates that these sites are the best hibernacula because they both protect from extreme winter temperatures and are close to breeding areas. On the other hand, use of a hibernaculum may be random, as indicated by the turtles that showed no obvious pattern of use (see also Brown and Brooks 1994). Moreover, communal hibernation can be problematic because of the potential to attract predators (Brooks et al. 1991).

The spotted turtle is a listed species throughout its range, and is currently considered "vulnerable" in Canada (Oldham 1991). Communal hibernation by turtles (this study; Behler 1996; Lewis and Ritzenthaler 1997; Perillo 1997) makes them susceptible to extirpation (Brooks et al. 1991). Habitat destruction or predation may result in the removal of a significant proportion of the breeding adults in a local population, as several communal hibernacula often exist in a single swamp. In addition, the spring aggregation of spotted turtles at breeding ponds makes them susceptible to collection. An alteration of the hydrology of the swamps or their hibernacula could pose a significant threat to population viability because alternative habitat or hibernacula may not be available or provide the necessary protection from predation and from extreme conditions in winter.

Acknowledgements

We thank F. Amtstaetter, C. Beckmann, J.H. Edmonds, and H.L. Passmore for help with field data collection. D. Golden and M. Wright helped digitize the map. J.T. Irwin reviewed an earlier draft of the manuscript. We are indebted to P. Marston for her generous support of this project and for providing accommodations for J.D.L. and Beckmann at Camp Hurontario. This research was supported by grants from the Endangered Species Recovery Fund of the World Wildlife Fund Canada to J.D.L. and R.J.B., the Environmental Youth Corps (Ontario Ministry of Natural Resources) to J.D.L. and R.J.B., the Natural Sciences and Engineering Research Council of Canada (A5990) to R.J.B., and the National Science Foundation (IBN 9507437) to J.P.C.

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