

Thermal Ecology of Blanding's Turtle in Central Minnesota

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ABSTRACT. – We studied daily and seasonal patterns of body temperature (T_b) in free-ranging Blanding's turtles (*Emydoidea blandingii*) in central Minnesota at the northwestern edge of the species' range. We recorded the internal T_b of 29 turtles (11 males, 17 females, 1 juvenile) living in shrub swamps for intervals of 1 to 15 months, for two summers and an intervening winter, via surgically implanted, temperature-sensitive data loggers. External shell temperatures were monitored with temperature-sensitive radio transmitters. Turtles were active from May to October, and they exhibited three daily patterns of T_b : thermoregulating (T_b max–min >11°C), thermoconforming (T_b max–min <6°C), and intermediate (11°C > T_b max–min >6°C). A daily sequence consisted of: a rapid or gradual heating phase, a plateau phase, a rapid cooling phase, followed by a prolonged phase of gradual cooling. On clear sunny days, the dominant pattern changed seasonally. In May, most turtles (90%) thermoregulated, whereas in July–October, only about half (45%) did. During November–April, turtles overwintered underwater beneath ice at T_b <2°C. Sex differences in thermal behavior were apparent. In comparison with males, females thermoregulated more often and maintained higher T_b in the fall, but not in the spring. These differences may reflect different reproductive activities. The T_b of this aquatic turtle was dependent on water temperature and on exposure to solar radiation mediated by basking behavior. Blanding's turtle is an active thermoregulator in a northern climate. Our study highlights the profound influence of water temperature on turtle T_b throughout the annual cycle. Relevant conservation concerns include minimizing disturbances to thermoregulating turtles, and maintaining intact and diverse aquatic habitats in suitable wetlands.

KEY WORDS. – Reptilia; Testudines; Emydidae; *Emydoidea blandingii*; turtle; ecology; thermoregulation; body temperature; thermal behavior; radiotelemetry; basking; overwintering; Minnesota; USA

Blanding's turtle (*Emydoidea blandingii*) is characterized as a northern species that inhabits productive, eutrophic wetlands from Quebec to Ontario southwest to Nebraska and southeast in the Great Lakes region eastward to New England (Ernst et al., 1994). In comparison with other freshwater turtles that range farther south, the species has low thermal thresholds (Hutchinson et al., 1966), selects low body temperatures (Nutting and Graham, 1993), and has been characterized as an aquatic species that may not regularly bask (Nutting and Graham, 1993). These factors may restrict Blanding's turtles to northern latitudes, but detailed information on the thermal regimes, requirements, and responses of the species are lacking, particularly along the northern edge of its range where the annual cycle of activity is six months or less (Ernst et al., 1994).

Given the pervasive effects of temperature on the energetics of freshwater turtles (e.g., Parmenter and Avery, 1990; Spotila et al., 1990), it is likely that specific features of Blanding's turtle energetics, involving maintenance, growth, reproduction, and storage, are directly and/or indirectly tied to the species' thermal ecology (Congdon, 1989). These factors, in turn, ultimately shape many life history attributes in this long-lived, late-maturing species (Congdon, 1989; Congdon et al., 1993; Congdon and Gibbons, 1996). In addition, conservation concerns include the need to pre-

serve sufficient habitat mosaics of uplands and wetlands. The thermal characteristics of the inhabited wetlands, in turn, are likely to have determinant effects on the energetics of a species as a function of its thermal response, particularly how it behaves in aquatic habitats.

Although Blanding's turtle habits are not well documented, due in part to the species' cryptic and secretive behavior, individuals not only bask out of the water (Pappas and Brecke, 1992; Ernst et al., 1994), but also have been observed swimming beneath the ice in winter (Evermann and Clark, 1916; Sexton, 1995) and basking directly on the ice margins of overwintering ponds (M. Pappas and B. Brecke, unpubl. obs.). These observations suggest that the species does, in fact, actively thermoregulate by basking, whereas other workers have suggested a more passive thermal strategy (Nutting and Graham, 1993). Basking is a common denominator and nearly a ubiquitous behavior among freshwater turtles, even though its biological significance and/or functions are debated and may vary with species and/or locality (Boyer, 1965; Moll and Legler, 1971; Auth, 1975; Schwarzkopf and Brooks, 1985; Manning and Grigg, 1997; Swimmer, 1997; additional references cited in Congdon, 1989). At northern latitudes in North America, basking is a frequent and dominant activity not only in a species that basks elsewhere in its range, e.g., painted turtles

(*Chrysemys picta*) (Schwarzkopf and Brooks, 1985; Lefevre and Brooks, 1995; Krawchuk and Brooks, 1998), but also in a species that seldom basks farther south in its range, e.g., snapping turtles (*Chelydra serpentina*) (Obbard and Brooks, 1979; Brown et al., 1994; Ernst et al., 1994). In contrast, the extent to which Blanding's turtles rely on basking as a thermoregulatory strategy, and its efficacy in terms of energetics across the species' range are poorly understood, but important features of the species' life history.

In Minnesota, detailed observations on marked individuals in a large population (Pappas et al., 2000) indicate that adult Blanding's turtles are noticeably more active at lower ambient temperatures than are painted or snapping turtles living side by side in the same wetlands. In southeastern Minnesota, Blanding's turtles are active at least several weeks earlier in the spring and later in the fall than are individuals of either of these more northerly distributed aquatic turtles (M. Pappas and B. Brecke, *pers. comm.*; J. Lang, unpubl. obs.). On these bases, we hypothesized that Blanding's turtles in central Minnesota would bask regularly to elevate and maintain body temperature above ambient thermal regimes, particularly above water temperature. We also predicted that seasonal changes in thermal behavior were likely, in response to seasonal warming and cooling of the aquatic habitats where the turtles lived. In addition, we anticipated that there would be sex-specific as well as individual differences in thermal responses among turtles, reflecting in part different energetic demands as well as the complexity of thermal responses in this northerly distributed species.

Earlier studies of turtle body temperatures (T_b) were based on spot measurements of cloacal temperatures (e.g., Moll and Legler, 1971; Ernst, 1972, 1982). Such approaches have been problematic. First, T_b measurements were intermittent because handling typically disrupted behavior. Second, disturbed turtles either quickly re-entered the aquatic environment, or dove to deeper water. Lastly, measurements focused on active or basking animals. However, estimates of the T_b of inactive or dormant turtles, in the evenings and during prolonged periods of overwintering, are also important components of annual energetics (Peterson et al., 1993).

Only recently has the T_b of free-ranging turtles been studied, by employing temperature-sensitive sensors incorporated into radio transmitters to take temperature measurements of turtles undisturbed in their environments (Brown et al., 1990; Brown and Brooks, 1991; Manning and Grigg, 1997). Miniature data loggers are now available that may be attached externally and/or implanted (Litzgus et al., 1999; Vitt and Sartorius, 1999). Using these methodologies, we investigated the patterns of T_b and thermal behaviors of a population of free-ranging Blanding's turtles in relatively undisturbed wetlands in central Minnesota. Our objectives were: (1) to describe turtle T_b and behaviors within the range of environmental temperatures available from day to day, (2) to investigate how turtles responded to seasonal and annual changes in temperature, (3) to compare the thermal responses of males and females throughout the annual cycle,

and (4) to characterize the thermal responses of Blanding's turtles in relation to other turtles.

MATERIALS AND METHODS

Study Site. — Camp Ripley (46°7'N, 94°22'W) is a military training site in Morrison County, 16 km north of Little Falls in central Minnesota, USA. It is bounded on the north by the Crow Wing River and to the east by the Mississippi River, and covers 21,500 ha. The region is a transition zone of three major ecosystems: southern deciduous forests, northern coniferous forests, and prairie (Tester, 1995). The topography is steep knob and kettle terrain; elevations range from 340–470 m.

The wetlands include alder and willow shrub swamps, mixed emergent wetlands created by beaver impoundments, ephemeral shallow wetlands, and open water lakes. In the southwest, there is an extensive wetland complex, mostly of shrub swamp, drained by Hay Creek. In the north and east, an expanse of wetlands drain into the Crow Wing and Mississippi Rivers. The dominant plants are willow, alder, tussock sedges, bulrushes, and cattails. Aquatic vegetation includes yellow pond lily, pond weed, elodea, and coontail (Minnesota DNR, 1993). Wetland substrates are typically poorly drained sandy soils covered by a thick layer of soft sedge peats. All of the wetlands are protected from military activities.

Upland habitat consist of forest regions, open fields, and cleared training ranges and impact areas. Forest stands are a combination of fragmented and contiguous tracts of mixed hardwoods and conifers. Open fields are maintained by clear cutting, burning, and military training activities and consist mainly of short grasses, small shrubs and forbs along with small open pockets of sand and mounds. Secondary roads and armor trails are scattered throughout the tract; sections of the upland are managed for forestry.

Methodology. — We collected turtles in aquatic hoop traps or by hand capture during road surveys, primarily in the nesting season. We measured and weighed captives, and recorded the sex, age, reproductive status, time, and location of capture. We determined age by counting annual growth rings on the plastron. In this population, juveniles were <210 mm in carapace length (= CL) (Sajwaj et al., 1998). Average body sizes of adults at Camp Ripley are larger than those studied elsewhere; CL of males = 260 mm ($n = 23$) and of females = 245 mm ($n = 42$) (Sajwaj et al., 1998). Sex was determined by presence of a plastral concavity and a greater preanal tail length in males. Female reproductive status was determined by palpation. Each turtle was marked on the marginal scutes of the carapace (Cagle, 1939). A radio transmitter was affixed using a fast drying epoxy compound, midway between the dorsal line and marginal scutes (Belzer and Reese, 1995), and the turtle released at the point of capture within 1–3 days.

Internal body temperature (T_b) was recorded with a data logger (TidBit, Onset Computer Corporation), surgically inserted into the body cavity via the inguinal cavity, anterior

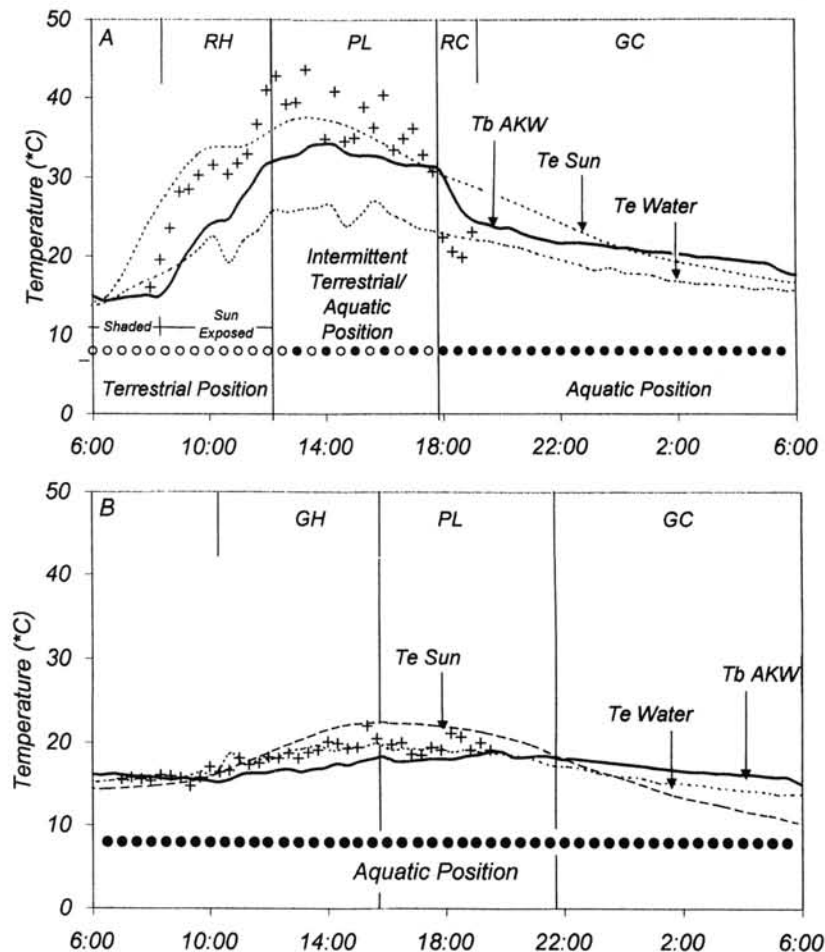


Figure 1. (A) Daily pattern of thermoregulation of a Blanding's turtle (adult female AKW; CL = 265 mm, 2.5 kg) on a sunny day (time of day on horizontal axis) during mid-July 1997. The daily pattern was subdivided into four phases: RH = rapid heating, PL = plateau, RC = rapid cooling, and GC = gradual cooling. T_b = dark solid line; T_e sun (model on land) = broad, broken line; T_e water (model in water) = short, broken line; external shell temperatures (T_s = +); land-water positions throughout the day are indicated below T_b record. (B) Daily pattern of thermoconformity shown for a Blanding's turtle (adult female AKW; CL = 265 mm, 2.5 kg) on an overcast day (time of day on horizontal axis) during mid-July. The daily pattern was subdivided into three phases: GH = gradual heating, PL = plateau, and GC = gradual cooling. T_b = dark solid line; T_e sun (model on land) = broad, broken line; T_e water (model in water) = short, broken line; external shell temperatures (T_s = +); land-water positions throughout the day are indicated below T_b record.

to the hind leg. The logger recorded turtle T_b every 24–72 min; each logger was calibrated for accuracy (0.2 to 0.4°C) before and after use. Turtles resumed normal activities, including nest digging and egg laying, within 1–3 days of implantation. There were no signs of ill health, infection, weight loss, or impaired movement. Additional details regarding implantation were described in Sajwaj (1998). For each turtle, external shell temperature (T_s) was recorded manually by monitoring the pulse rate of a temperature-sensitive circuit incorporated into a radio transmitter. Each circuit was calibrated and was accurate to $\pm 0.2^\circ\text{C}$.

Turtle-shaped models (each constructed of a 5 mm thick fiberglass carapace and plastron molded on actual shell forms, painted with matt brown-black paint, filled with water, and equipped with a centrally-located, temperature-sensitive data logger) were used to estimate environmental temperature (T_e). Models of a small, medium, or large individual in this population (1.3, 1.8, or 2.3 kg, respectively) were placed in representative microhabitats, in various positions in water and on land (Peterson, 1987; Grant

and Dunham, 1988; Bakken, 1992; Vitt and Sartorius, 1999). On a given day, nine models were used to monitor the effective T_e in each of two locations within the wetland where the monitored turtles resided. In each location, small, medium, and large models were positioned within 10 m of each other to be completely on land, partially on land, or submerged in water. On a sunny day with little wind, the heating rates of live unrestrained turtles closely tracked those of similar sized models in identical positions on land and/or in the water ($r^2 > 0.95$, $p < 0.01$). In addition, standard environmental temperatures were recorded in representative wetlands in shaded air at 40 cm above the water surface, and in the water (T_w) at depths of 0.1 and 0.9 m. Additional detail on the T_e models was given by Sajwaj (1998).

Non-parametric tests were used to detect differences in daily T_b pattern occurrence, daily maximum T_b , and daily phase characteristics between adult males and females because sample sizes were small and not necessarily normally distributed (Sokal and Rohlf, 1995). Correlation coefficients were calculated using standard regression analysis.

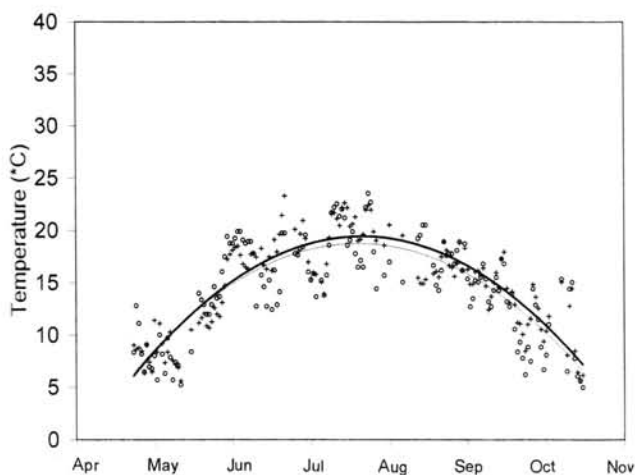


Figure 2. Seasonal trend in daily minimum water temperatures (T_w = +) was plotted across the activity season (April through October; horizontal axis) and fitted by interpolation with a curved line (thick line). Daily minimum body temperatures (T_b = o; trend line = thin line) tracked the seasonal increase through July as well as the seasonal decrease through October. T_b shown here for 8 adult turtles living in Range Marsh in 1997, based on 692 daily records of 3 males and 5 females.

Analyses were performed with Statmost and Excel statistical software. Unless otherwise noted, the significance level was $\alpha = 0.05$.

RESULTS

We studied 29 turtles (11 males, 17 females, 1 juvenile) from May 1996 to October 1997 at Camp Ripley. Individuals were monitored for intervals of 1 to 15 months, resulting in 153,000 T_b measurements over the equivalent of 5630 turtle-days (Sajwaj, 1998). The daily T_b records for many of these turtles extended over two activity seasons (May through September) and the intervening winter. The results presented here are representative, and are based primarily on the daily records of 8 adults (3 males and 5 females) that inhabited Range Marsh, an 18 ha shrub swamp. In our analysis, each daily record of turtle T_b was classified as thermoregulating, thermoconforming, or as an intermediate pattern. For each of these patterns, characteristic thermal features were associated with the daily phases of rapid or gradual heating (morning), plateau (midday), rapid or gradual cooling (late afternoon), and gradual cooling (evening and at night). In the following section, the daily records of one of these turtles, judged to be "typical," are presented graphically and explained; then the quantitative features of the daily phases associated with each daily thermal pattern are summarized, based on the data for all of the turtles studied in Range Marsh. Additional thermal data and analyses, not presented here, were included elsewhere (Sajwaj, 1998).

Daily Patterns of Body Temperature. — The sample daily record of T_b for an adult female turtle on a clear, sunny day in mid-summer is shown in Fig. 1A. During rapid heating in the morning, T_b increased at a rate of 4.6°C/hr for 2.7 hrs. The turtle's rate of heating approximated the heating

rate of a turtle model (T_c) positioned on land in the sun. By midday, the turtle's shell temperature (T_s) had risen rapidly to 35–40°C. On the basis of measured T_s and in comparison with turtle models in and out of the water, the turtle was completely out of the water on land and exposed to sun throughout the morning (Fig. 1A).

After midday, the turtle's external T_s began to fluctuate, sometimes by as much as 10°C (at ca. 1400 hrs), indicating that it was actively moving in and out of the water, alternating its exposure to solar radiation. By contrast, the turtle's internal T_b was relatively stable and averaged 32.5°C for 6 hrs (Fig. 1A). By early evening, the turtle's external T_s quickly dropped to water temperature, indicating that it had moved into the water from a position on land. During this rapid cooling phase, the turtle's T_b decreased at a rate of 5.4°C/hr for 1.2 hrs. Throughout the night, the turtle's T_b declined slowly at a rate of 0.5°C/hr, for 13.2 hrs. During this gradual cooling phase, the turtle's T_b closely paralleled the slow decline in water temperature during this period, indicating it was submerged in the water (Fig. 1A). This was the typical daily cycle of T_b , a pattern we refer to as a thermoregulating pattern. It occurred on sunny days and was characterized by a daily range in T_b that exceeded 11°C (difference between maximum and minimum T_b). During the activity season, thermoregulation was the dominant daily T_b pattern observed in the turtles we studied.

A sample daily T_b record for the same adult female on an overcast day in mid-summer is illustrated in Fig. 1B. This pattern of T_b occurred on days when solar radiation was limited or absent, and was observed infrequently. The daily range of T_b was 6°C or less (difference between maximum and minimum T_b). Because the turtle's T_b remained close to ambient water temperature throughout the day, we refer to this pattern as thermoconforming. It was characterized by

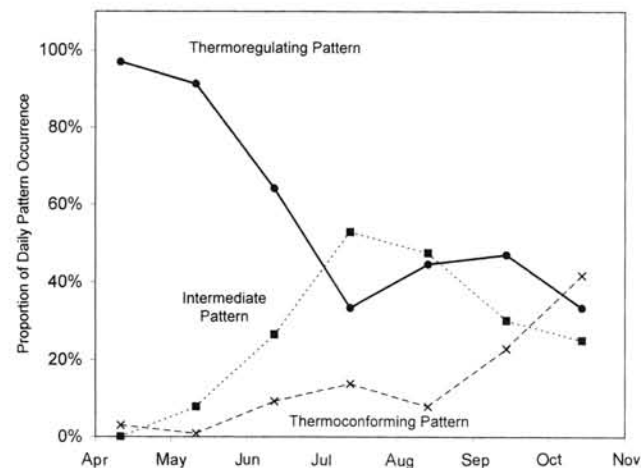


Figure 3. Seasonal changes in daily patterns of body temperature (T_b) of adult Blanding's turtles on sunny days throughout the activity season, adjusted monthly to equalize records for each sex. Shown by month is the proportion of turtles exhibiting the thermoregulating pattern (solid line, ●), thermoconforming pattern (broken line, x) and intermediate pattern (broken line, ■). This analysis was based on 794 daily records of 17 adults (5 males, 12 females) monitored in 1997.

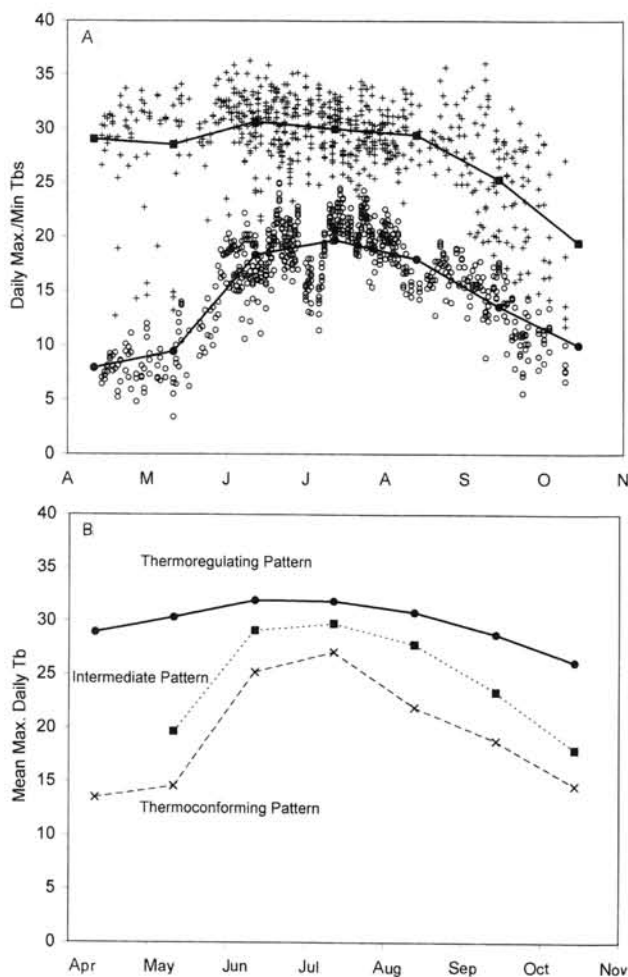


Figure 4. (A) Seasonal changes in daily maximum (+) and minimum (o) body temperatures (T_b) for 8 adult Blanding's turtles living in Range Marsh. Daily minimum T_b increased from April through July, then decreased from August through October. In contrast, daily maximum T_b was consistently high (ca. 28–32°C) in the spring and summer, but decreased (ca. 20–25°C) in the fall. This analysis was based on 692 daily records of 3 males and 5 females, as in Fig. 2. Monthly means are connected with trend lines; monthly means are shown for daily maximum T_b (■) and daily minimum T_b (●). (B) Seasonal changes in body temperature (T_b) associated with the daily patterns of thermal behavior shown by adult turtles during the activity season. The mean monthly maximum T_b associated with thermoregulation (solid line, ●), thermoconformity (broken line, x) and the intermediate pattern (broken line, ■) were plotted for April through October. The strongest seasonal effects were evident with the two latter patterns, associated with predominately aquatic daytime activity. In contrast, thermoregulation exhibited only slight seasonal effects.

three daily phases (gradual heating, plateau, and gradual cooling) that were difficult to distinguish. During the morning heating phase, the turtle's T_b increased only 1.0°C/hr for 4.8 hrs. By midday, the mean T_b was 18.3°C during a plateau phase that lasted 5.6 hrs. During the gradual cooling phase, the turtle's T_b decreased 0.3°C/hr over 11.8 hrs by late evening. All of these phases were associated with rates of heat exchange that indicated that the turtle remained in water throughout the day (Fig. 1B).

On partially cloudy days, an intermediate pattern of daily T_b was evident. The observed range was less than 11°C but greater than 6°C for the daily change in T_b . The turtle's

position in the water was partially exposed, based on a comparison of turtle T_b to model T_e . Movements on to land, when they did occur, were timed to coincide with intermittent sunshine. Examples of the intermediate pattern are not included here, but were presented by Sajwaj (1998). During the rapid heating phase, thermoregulating turtles warmed at rates similar to those of models positioned on land on sunny days; whereas thermoconforming turtles exhibited little or no heat gain on overcast days. During the plateau phase, mean T_b was highest on sunny days, lower on partly cloudy days, and close to water temperature (T_w) on overcast days. Rates of gradual cooling were similar, regardless of weather differences, in the evening and at night, and paralleled the nocturnal decline in wetland T_w .

Seasonal Influences on Body Temperature. — We examined the daily T_b records and patterns of thermal behavior for seasonal changes. Because these turtles were predominantly aquatic, water temperature (T_w) was an important thermal factor. Daily minimum T_w typically occurred at sunrise, by which time a turtle's T_b had equilibrated with T_w . In this analysis, we examined the T_b records of 3 males and 5 females that occupied Range Marsh. When plotted, a strong positive linear relationship ($r^2 = 0.812$, $p < 0.01$) was observed between daily minimum T_w and the turtles' daily minimum T_b (Fig. 2).

The daily pattern of thermal behavior and T_b changed during the activity season. In April and May, daily minimum T_w was ca. 10°C; at this time, >90% of turtles exhibited daily T_b patterns that indicated active thermoregulation. In July and August, daily minimum T_w was ca. 20°C; the proportion of thermoregulating turtles on sunny days dropped to 33%. In September and October, daily minimum T_w cooled to ca. 10°C; only 33–47% of turtles thermoregulated; the remainder thermoconformed or showed an intermediate pattern of daily T_b . This result was in contrast to the response in the spring when most turtles thermoregulated (Fig. 3).

The seasonal shift from thermoregulation in the spring to thermoconformity in the fall was evident as a seasonal shift in daily maximum T_b (Fig. 4A). From April through August, mean daily maximum T_b was 29.9°C ($n = 580$, SEM = 0.13). During September, it decreased to 25.3°C ($n = 96$, SEM = 0.49), and then to 19.5°C ($n = 16$, SEM = 1.45) during early October. Seasonal effects were also evident in the maximum T_b achieved via each of the three daily T_b patterns during the activity season. Mean maximum T_b achieved via the thermoregulating pattern increased from 28.9°C in spring, to 31.9°C in summer, then decreased to 26.2°C by fall. For the thermoconforming pattern, mean maximum T_b increased from 13.5°C in spring, to 27.1°C by mid-summer, and then declined to 14.7°C by fall (Fig. 4B).

Sex Differences. — From April through August, no differences were evident in the proportions of males vs. females that thermoregulated. However, in September and October, females thermoregulated more than males (MWU-test; September, $p < 0.01$; October, $p = 0.049$; Fig. 5A). Although the observed differences in thermal behavior re-

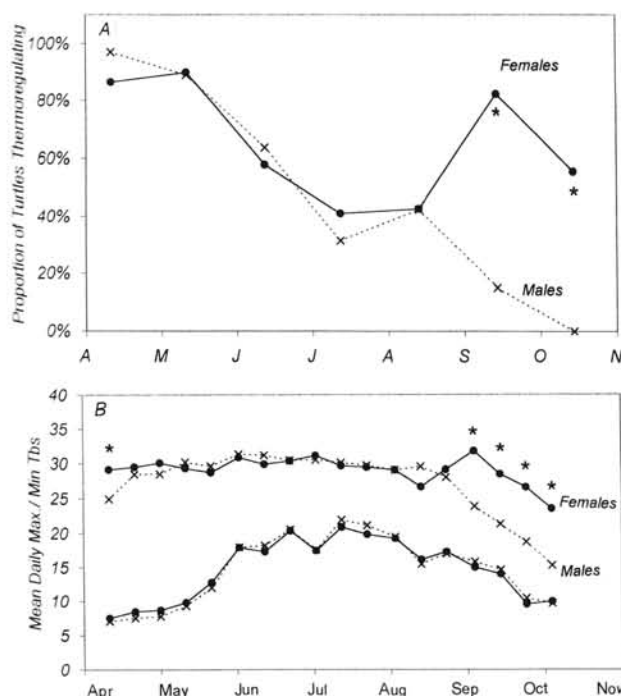


Figure 5. (A) Sex differences in thermal behavior of Blanding's turtles. The proportion of males (broken line, x) and females (solid line, ●) exhibiting the thermoregulating pattern on sunny days was plotted across the activity season. Significant differences between males and females are indicated by an asterisk (Mann-Whitney U-test). (B) Sex differences in body temperatures (T_b) of Blanding's turtles. Mean daily maximum and minimum T_b of males (broken lines, x) and females (solid lines, ●) were plotted across the activity season. No significant differences were observed in daily minimum T_b . Females exhibited significantly higher maximum T_b (*) than males in April and in September–October (Mann-Whitney U-test). This analysis included 16 individuals from a variety of wetlands (5 males, 11 females), and 1192 daily records (408 male records, 784 female records).

sulted in sex differences in maximum daily T_b for females vs. males, daily minimum T_b did not differ. Similarly, daily maximum T_b of late April through late August were not significantly different. However, females exhibited significantly higher maximum T_b during mid-April and in September and October (MWU-test; $p < 0.05$; Fig. 5B).

The daily phase characteristics for males and females that exhibited the thermoregulating pattern showed that females consistently maintained longer plateau phases at higher T_b during April through August, but these differences varied. Females exhibited longer plateau phases in August (MWU-test, $p = 0.019$) and higher plateau temperatures in April ($p = 0.043$) and September ($p < 0.01$). In October, no males thermoregulated whereas some females did.

Annual Cycle of Body Temperature. — Cold temperatures constrained T_b during the winter months. All of the turtles that we monitored overwintered underwater at depths of approximately 1 to 1.5 m, beneath a layer of snow and ice that varied from 0.5 to 1 m in depth. Turtle T_b was at or below 2°C for at least 5 months, from November through March. Consequently, all of the turtles thermoconformed during this period (Fig. 6). Turtle T_b in Range Marsh during this period is shown for a representative male and female in Fig. 7.

Year-to-year comparisons are possible for the two activity seasons during which we monitored turtles. In general, based on their T_b records, males behaved similarly in 1996 and in 1997, whereas females in the same environments behaved differently from one year to the next. In 1996 as compared to 1997, considerably more females thermoregulated during July and August, while proportionately fewer females thermoregulated during September (Fig. 6A). In both years, females thermoregulated more than males during the summer months; and in the fall, similar differences were evident, as noted above (Fig. 6A). Males showed a different pattern of thermal behavior that changed seasonally, but was consistent from 1996 to 1997, based on the relative occurrence of T_b patterns (Fig. 6B).

Year-to-year differences were also evident in the maximum T_b achieved by males and by females. In 1996 vs. 1997, males exhibited higher maximum T_b during May and June, but lower T_b during July. In 1996 vs. 1997, females exhibited higher T_b during August, but lower T_b during September and October. Females consistently exhibited higher maximum T_b during September and October of both years, in comparison with those of males (Table 1). These differences are evident in the T_b records of a representative male and female turtle inhabiting Range Marsh (Fig. 7).

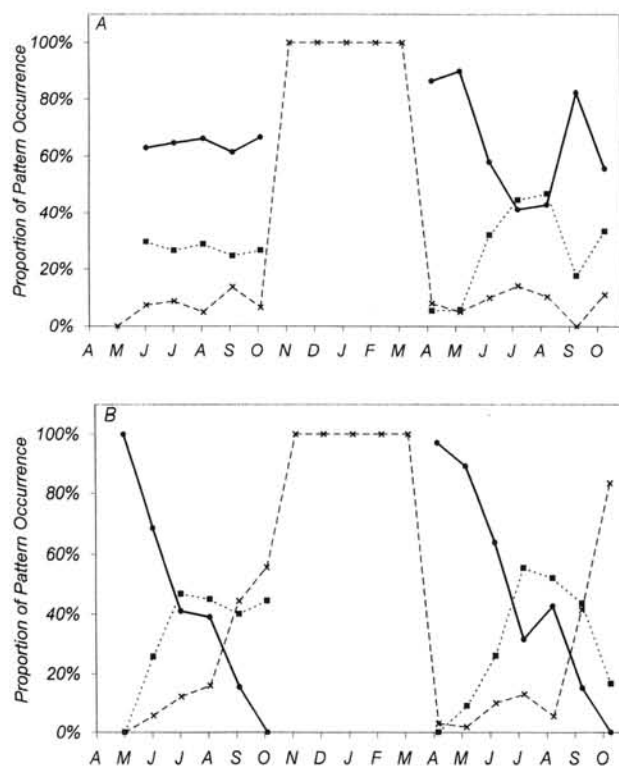


Figure 6. (A) Annual change in female thermal behavior. The proportion of females exhibiting the thermoregulating (solid line, ●), thermoconforming pattern (broken line, x) and intermediate pattern (broken line, ■) during sunny days was plotted across the activity seasons of 1996 and 1997. The intervening winter, November–March, constrained thermal behavior, and was labeled thermoconforming. (B) Annual change in male thermal behavior. Symbols as in (A) above.

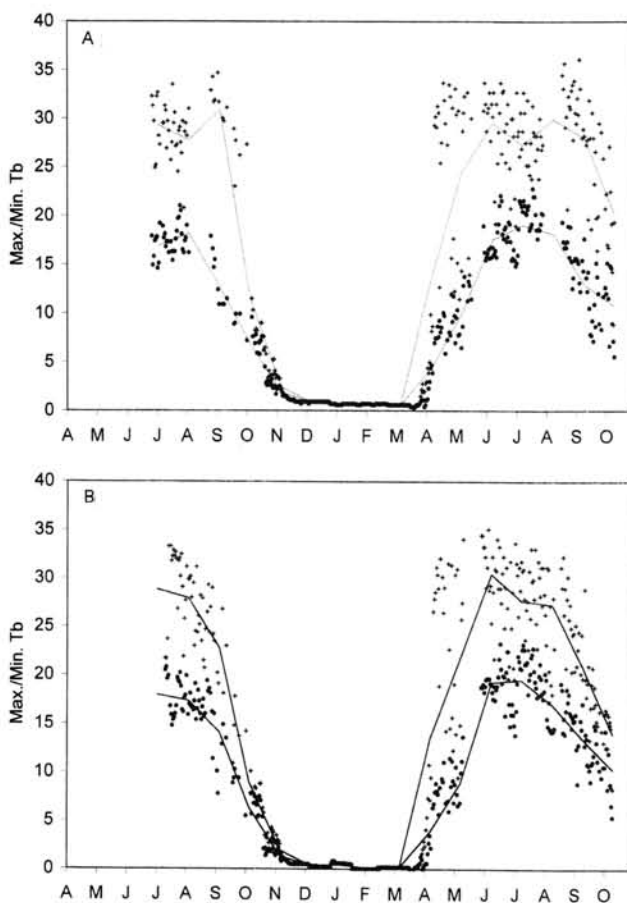


Figure 7. (A) Female body temperatures during the annual cycle for a Blanding's turtle in central Minnesota. Daily minimum (●) and maximum (+) T_b of a female exemplify the changes in T_b during the year. In fall, females were more likely to exhibit higher maximum T_b than males. (B) Male body temperatures during the annual cycle for a Blanding's turtle in central Minnesota. Daily minimum (●) and maximum (+) T_b of a male exemplify the changes in T_b during the year. In fall, males were more likely to exhibit lower maximum T_b than females. These records are for 2 adults living in Range Marsh in 1996 and 1997.

DISCUSSION

Daily Pattern of Body Temperature. — Blanding's turtles in central Minnesota were aquatic, except for brief, occasional trips overland (Piepgras, 1998; Piepgras and Lang, 2000). Seasonal activities such as foraging, mating, and overwintering occurred in the water. Turtles were typically active during the daytime and inactive at night (Sajwaj et al., 1998; Piepgras et al., 1998). During the gradual cooling phase, turtle T_b decreased and eventually equilibrated by sunrise with T_w , indicating that turtles were in aquatic positions during the late evening and early morning. As a consequence, all of the turtles in a wetland started each day with a minimum T_b that was nearly equivalent, e.g., minimum T_b did not differ (Figs. 2 and 5B), regardless of whether a turtle's T_b had been high or low the previous day. When turtles thermoconformed on overcast days, their T_b tracked T_w closely. Typically, T_b decreased with T_w during the early morning and then

Table 1. Year-to-year comparisons of mean daily maximum T_b on sunny days for males and females (grouped by sex by month) are summarized for 1996 vs. 1997. For each sex, same months were compared for significant differences between years, indicated by an asterisk (Mann-Whitney U-test).

Month	Males		Month	Females	
	1996	1997		1996	1997
May*	31.5	29.4	May	n/a	28.9
June*	31.6	31.0	June	30.6	30.1
July*	27.9	30.2	July	29.7	29.9
August	27.9	28.5	August*	29.5	27.6
September	23.5	21.7	September*	26.2	28.6
October	13.8	15.2	October*	21.6	23.7

warmed as T_w warmed slowly. These turtles likely remained in the water all day. By evening, their declining T_b paralleled the gradual drop in T_w .

On sunny days, the turtles in our study thermoregulated at relatively high T_b . Comparison of the T_b of free-living, monitored turtles with those of similarly-sized models positioned on land in the sun indicated that such high T_b were only available to turtles that emerged out of the water. Movement onto land coincided with rapid heating during mid-morning, and this phase often lasted for 3+ hours. Later, during the plateau phase, a turtle frequently shifted positions between land and water to maintain T_b at plateau levels, based on frequent and rapid changes in shell temperatures (T_s). Additional data collected for some turtles support this interpretation. Mean activity levels, monitored via sensors incorporated into the radio transmitters of some turtles, were highest at high T_b associated presumably with frequent land-water movement, and lowest at low T_b associated with presumably stationary positions submerged in the water (Sajwaj et al., 1998).

When conditions were permissible, Blanding's turtles in central Minnesota consistently decoupled T_b from ambient air and water temperatures by land-water movements. We attribute a thermoregulatory function to such behavior because a turtle typically warmed quickly to a high T_b that was maintained for hours each day. Whether a turtle seeks heat may depend on a wide range of external and/or internal factors. For instance, the mean plateau temperatures of free ranging Blanding's turtles in our study were higher than the preferred temperatures reported for captive adults in a laboratory thermal gradient (Nutting and Graham, 1993). This disparity may be attributable not only to differences in lab vs. field conditions, but also to nutritional status and/or to regional differences in thermal response. The animals in the thermal gradient trials were denied food for 7 days before testing. Thermophily following feeding is now well documented in certain reptiles (Gatten, 1974; Lang, 1987; Dorcas et al., 1997). Our preliminary data, based on stomach flushing throughout the season, indicated that sampled (>75%) turtles contained food, primarily aquatic invertebrates (Sajwaj et al., 1998). This observation, in turn, suggests that the free-living turtles at Camp Ripley may maintain high T_b to improve metabolic and digestive efficiency (Huey, 1982; Hammond et al., 1988). Other internal factors that may have

altered the thermal responses of the turtles that we studied were age, sex, reproductive condition, and/or health status (Peterson et al., 1993). Finally, a probable thermoregulatory function does not preclude other beneficial consequences of moving out of the water on to land (reviewed in Congdon, 1989; Manning and Grigg, 1997; Swimmer, 1997).

Thermoconformity typically occurred on overcast days, but was sometimes observed on clear sunny days. On these days, the turtle remained in the water despite the likelihood of increasing T_b by moving onto land. The intermediate pattern, characteristic of partly cloudy days, was also observed on sunny days. These instances of turtles foregoing opportunities to thermoregulate (= voluntary thermoconformity), presumably in favor of other activities, suggest that the thermal responses of these turtles were complex, and subject to factors beyond the proximate constraints of the immediate thermal environments available to them.

Seasonal Changes in Body Temperature. — As daily minimum T_w increased from 10 to 20°C from spring to summer, the thermal behaviors of turtles changed. During May and early June, most (ca. 90%) of the turtles thermoregulated on sunny days. By July, fewer turtles (ca. 40%) thermoregulated by warming on land, and the intermediate pattern associated with only partial emergence was common. In addition, the duration of the rapid heating phase decreased, while the duration of the plateau phase increased. Although the daily sequence and timing of thermal behaviors changed from spring to summer, daily maximum T_b averaged 30.3°C in the spring and 31.9°C in the summer. Consequently, these turtles were able to maintain daily T_b within a range of 1.6°C, despite a seasonal change of 10°C in T_w from spring to summer.

Early in the season when T_w was 5–15°C, the major behavior was movement into and out of the water once high T_b was achieved during the midday hours of sunny days. Such behavior resulted in stable T_b ranging from 15.3 to 34.9°C (median = 29.3°C; $n = 384$) for intervals of 1.2–9.6 hours. During the plateau phase, T_b was 3.6 to 7.7°C higher than the T_e of models positioned in the water. Later in the season when T_w was warmer (15–22°C), turtle T_b could be maintained by aquatic basking (= partially emergent positions on land) or intermittent land-water movements, based on the thermal responses of models in various positions. In other aquatic turtles, emergence onto land (i.e., atmospheric basking) most commonly occurred on clear sunny days when T_b was likely to be elevated above ambient environmental temperatures (Boyer, 1965; Auth, 1975; Crawford et al., 1983; Schwarzkopf and Brooks, 1985; Di Trani and Zuffi, 1997; Litzgus and Brooks, 2000).

In spring, elevated $T_b > 27^\circ\text{C}$ was available only to turtles that spent hours every day out of the water. Turtles were forced to choose between thermoregulation and the attendant high T_b , or the low T_b associated with remaining in the water, e.g., thermoconformity at T_w of $< 20^\circ\text{C}$. By mid-summer, thermoconformity and/or an intermediate pattern resulted in T_b of 27 and 30°C, respectively. Hence, turtles were able to maintain relatively high T_b , without moving

completely onto land. As a consequence, more time could be spent in aquatic habitats, e.g., foraging.

As T_w cooled from summer to fall, the turtles did not thermoregulate more frequently, as they tended to do at comparable T_w in the spring to summer transition. Rather, thermoconformity and/or the intermediate patterns were as common as the thermoregulating pattern. The maximum T_b achieved by turtles declined from July to October. The duration of the plateau phase decreased from July to October, while the duration of the rapid heating phase increased. These changes could be attributed simply to low ambient temperatures, i.e., environmental constraints; alternatively, they may reflect seasonal changes in thermal response.

Our observations support the latter interpretation. For example, on 20 of 23 clear days in September 1996, at least one of 5 turtles achieved a maximum $T_b > 28^\circ\text{C}$, suggesting that the environment did not limit turtles from reaching warmer T_b . However, even on sunny days in October, daily maximum T_b was $< 26^\circ\text{C}$. Thus, despite cool T_w and T_b in the fall, turtles did not thermoregulate as readily and/or as often as in the spring. The question then becomes why would a majority of turtles in a northern population forego opportunities to elevate T_b ?

Sex Differences in Body Temperature. — In our study, we found little difference in the thermal behaviors and T_b of males and females in the spring and summer. However, during September and October, females thermoregulated but males did not, resulting in different thermal patterns and T_b for each sex. Various studies with aquatic turtles have attempted to identify sex differences in thermal behavior, the frequency and duration of basking episodes (Lefevre and Brooks, 1995; Krawchuk and Brooks, 1998), and sex differences in thermal selection in a thermal gradient (Hammond et al., 1988; Nutting and Graham, 1993) with varying degrees of success. The sex differences we noted may have several explanations, none of which are mutually exclusive. These include the following: (1) females may thermoregulate more because of activities associated with reproduction, and (2) males may thermoregulate less because of activities associated with reproduction. In Blanding's turtles, courtship and mating occur in the water (Baker and Gillingham, 1983), and so would not be compatible with the frequent land-water movements necessary to thermoregulate at low T_w .

Thermoregulation may compete with male reproductive activities such as mate-seeking. During spring and fall, hoop traps containing only adult females captured adult males (Sajwaj et al., 1998). Males may locate receptive females by using aquatic olfactory cues. On 6 October, we discovered two pairs of mating turtles by recovering a radiotagged member of each pair. These observations suggest that some turtles at Camp Ripley court and mate prior to overwintering. At Camp Ripley, males moved more in early fall than did females (Piegras, 1998; Piegras and Lang, 2000). These sex differences in various behaviors suggest that, in our study, males may relax thermoregulation in favor of finding and acquiring mates.

The energetic demands of egg production may also explain such sex differences. Certain sex differences were noted in basking behavior of male vs. female painted turtles (*Chrysemys picta*), but others were not evident, despite expectations to the contrary (Lefevre and Brooks, 1995; Krawchuk and Brooks, 1998). These studies were conducted from May to August in the same year the eggs were laid, typically in early summer. In another study on *C. picta* in a northern location, follicular development was found to occur from August to October of the previous year (Congdon and Tinkle, 1982). This result, in turn, suggests that sex differences in thermal behaviors that are related to reproduction, such as egg production, may be more apparent in the fall than in the spring. Follicular development in the late summer and fall is well documented in other north-temperate aquatic turtles; unfortunately, the reproductive cycles of Blanding's turtles have not been documented (Ernst et al., 1994).

Thermal Strategies of Aquatic Turtles. — The thermal behaviors and T_b of the turtles were directly related to the annual cycle of water temperature in the wetlands they inhabited in central Minnesota. Regional differences in wetlands and in climate likely contribute to geographic differences in the thermal relations of Blanding's turtles from various localities. Thermal strategies likely differ among populations of Blanding's turtles elsewhere, but quantitative data are not yet available for meaningful comparisons with our study. Nevertheless, some generalizations are possible. Blanding's turtles in central Minnesota emerge early in the spring and retreat late in the autumn, are active at low water temperatures ($<10^\circ\text{C}$), bask regularly throughout the activity season, but show no indication of summer aestivation, either on land or in the water. In addition, females in this population thermoregulate more than males in the late summer and fall, but not in the spring and early summer. These features, either alone or in combination, distinguish this population on the northwestern edge of the species' range from populations studied elsewhere, notably those in Wisconsin (Ross, 1989; Ross and Anderson, 1990), Illinois (Rowe and Moll, 1991), Ontario (Petokas, 1987), Maine (Joyal, 1996), and Nova Scotia (Power, 1989).

Although we focused primarily on the thermal behaviors of active turtles, a prolonged period of inactivity, for at least 5 months at $T_b < 2^\circ\text{C}$, is a critical component of the annual thermal cycle for this north-temperate reptile. The turtles we monitored spent the winter underwater in shallow wetlands, at 1 to 1.5 m depths beneath a variable layer of ice and snow at 0.5 to 1 m depths. Turtles remained buried in mud and organic debris on the wetland bottom, and showed little evidence of any movement throughout the period of submergence (Piepgras, 1998; Piepgras and Lang, 2000). These hibernacula, typically located in shrub swamps, provided frost-free aquatic refuges that resulted in low T_b that depressed metabolism and consequently reduced energy expenditure over the long winter. Within these hibernacula, turtles did not have access to air, in contrast to hibernacula used by spotted turtles (*Clemmys guttata*) in Ontario (Litzgus et al., 1999). The underwater hibernacula in our study likely

facilitated additional energy savings by inducing anoxia and anaerobic glycolysis in a manner similar to that documented for other turtles overwintering at northern latitudes (Ultsch, 1989; Jackson, 2000). In the spring, early emergence coupled with frequent basking and attendant high T_b may be beneficial in order to rectify acid-base imbalance associated with prolonged hypoxia for these aquatic species that overwinter underwater (Ultsch, 1989).

Thermal strategies also differ among species of aquatic turtles living in north-temperate environments. At Camp Ripley as well as elsewhere in Minnesota where Blanding's turtles occur, painted turtles and snapping turtles are common, the three species coexisting in many wetlands. Most aquatic turtles can be categorized as "baskers" or "non-baskers," on the basis of whether or not time is spent on land exposed to solar radiation. In our study, painted turtles were often observed basking wherever they occurred, but snapping turtles were never observed basking. Although our thermal data indicate that Blanding's turtles in central Minnesota are "baskers," we rarely observed turtles in exposed positions, on logs or floating objects actively basking. Limited observations indicated that they basked on sedge mats and in protected openings where detection was especially difficult. In addition, the Blanding's turtles at Camp Ripley were extremely wary, and very easily disturbed when they were exposed.

Protection from disturbance may be an important conservation concern in wetlands subject to increasing levels of human activity, e.g., recreational fishing and/or boating. For example, frequent disturbance in a wetland inhabited by Blanding's turtles would likely result in frequent interruptions in basking. As a consequence, turtles may be prevented from elevating and/or maintaining T_b at preferred levels. Persistent interruptions would likely result in long-term and possibly detrimental energetic consequences, e.g., reduced rates of digestion and ingestion.

Another conservation concern highlighted by our study is the profound influence of water temperature on a turtle's T_b throughout the annual cycle. At our study site, most turtles resided in shrub swamps, and tended to remain longer and move farther in large vs. small swamps (Piepgras and Lang, 2000). In some instances, turtles remained in the same wetland throughout the annual cycle of activity and winter dormancy (Piepgras, 1998; Piepgras and Lang, 2000). Shrub swamps typically are complex assemblages of open water with aquatic and emergent vegetation interspersed with dense shrub thickets. Such wetland habitat provides a multi-layered, structured mosaic of aquatic and terrestrial microhabitats, characterized by a diversity of thermal environments. In particular, daily water temperatures set limits on the extent to which a turtle's T_b differs from that of the surrounding environment. Consequently, alterations in water level and/or in wetland vegetation and associated structure potentially influence the thermal responses of Blanding's turtles, with possibly detrimental energetic consequences. In energetic terms, harvesting and particularly processing rates associated with energy acquisition and assimilation

(Congdon, 1989) are likely to be negatively affected if thermoregulating turtles are disturbed and/or if wetland habitats are altered. If adverse conditions persist, survivorship and/or recruitment may be negatively affected, and the long-term viability of local populations of Blanding's turtles placed in jeopardy.

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